



THE UNIVERSITY OF KANSAS  
SCIENCE BULLETIN

Vol. 54, No. 7, pp. 209-256

MCZ  
LIBRARY May 31, 1991

JUN 19 1991

Classification and Phylogenetic Relationships of the  
Panurgine Bees: The Calliopsini and Allies  
(Hymenoptera: Andrenidae)<sup>1</sup>

BY LUISA RUZ<sup>2</sup>

CONTENTS

Abstract . . . . .	210
Introduction . . . . .	210
Materials and Methods . . . . .	210
Acknowledgments . . . . .	211
Subfamily Panurginae . . . . .	212
Key to Tribes Calliopsini, Protomeliturgini and Perditiini . . . . .	212
Tribe Perditiini . . . . .	213
Genus <i>Perdita</i> Smith . . . . .	213
Tribe Protomeliturgini . . . . .	215
Genus <i>Protomeliturga</i> Ducke . . . . .	215
Tribe Calliopsini . . . . .	217
Key to the Genera of the Tribe Calliopsini . . . . .	218
Genus <i>Acampopoeum</i> Cockerell . . . . .	219
Genus <i>Calliopsis</i> Smith . . . . .	222
Key to the Subgenera of the Genus <i>Calliopsis</i> . . . . .	223
Subgenera <i>Calliopsis</i> , 225; <i>Perissander</i> , 226; <i>Calliopsima</i> , 227; <i>Verbenapis</i> , 228; <i>Liopoeum</i> , 229; <i>Hypomacrotera</i> , 231; <i>Nomadopsis</i> , 232; <i>Macronomadopsis</i> , 234; <i>Micronomadopsis</i> , 235; <i>Liopoeodes</i> , new subgenus, 236; <i>Ceroliopoeum</i> , new subgenus, 237	
Genus <i>Arhysosage</i> Brèthes . . . . .	238
Genus <i>Spinoliella</i> Ashmead . . . . .	240
Key to the Subgenera of the Genus <i>Spinoliella</i> . . . . .	241
Subgenera <i>Spinoliella</i> , 242; <i>Peniella</i> , 242	
Genus <i>Callonychium</i> Brèthes . . . . .	242
Key to the Subgenera of the Genus <i>Callonychium</i> . . . . .	244
Subgenera <i>Callonychium</i> , 244; <i>Paranychium</i> , 244	
Cladistic Analysis . . . . .	244
Appendix: A New Species of Calliopsini from Argentina . . . . .	253
Literature Cited . . . . .	254

<sup>1</sup>CONTRIBUTION NUMBER 3044 FROM THE DEPARTMENT OF ENTOMOLOGY, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045.

<sup>2</sup>LABORATORIO DE ZOOLOGÍA, UNIVERSIDAD CATÓLICA DE VALPARAÍSO, AV. BRASIL 2950, VALPARAÍSO, CHILE.

## ABSTRACT

This is part of a taxonomic study of the genera and subgenera of the andrenid subfamily Panurginae. Three tribes are recognized and described here: Calliopsini (with two new subgenera and one new species), Protomeliturgini (*Protomeliturga*) and Perditini (*Perdita*). The Calliopsini includes *Acamptopoeum*, *Calliopsis* (*Calliopsis* s. str.), *C.* (*Perissander*), *C.* (*Calliopsima*), *C.* (*Verbenapis*), *C.* (*Liopoeum*), *C.* (*Hypomacrotera*), *C.* (*Liopoeodes*, n. subg.), *C.* (*Ceroliopoeum*, n. subg.), *C.* (*Nomadopsis*), *C.* (*Macronomadopsis*), *C.* (*Micronomadopsis*), *Arhysosage*, *Spinoliella*, and *Callonychium*. Extensive generic descriptions provide much more information than has been available in the past on the features of the taxa under study. Keys to all genera and subgenera of these tribes are included.

A cladistic analysis has been made in order to understand the relationships among the genera and subgenera of the Calliopsini and closely related taxa. At least some clarification of lines between genera has been attained. A broad interpretation of the genus *Calliopsis* is proposed. Illustrations for each genus-group taxon are provided.

## INTRODUCTION

The family Andrenidae contains two subfamilies: Andreninae and Panurginae. A study of the Panurginae at generic and subgeneric levels, with a classification and phylogeny of the included taxa, was presented by Ruz (1986). That study shows that the Panurginae is a monophyletic group and that several tribes can be recognized.

The Panurginae contains numerous genera and, like the Andreninae, is found in all continents except Australia. Its diversity and abundance, however, are greatest in the Western Hemisphere.

The present paper is part of the subfamilial study mentioned above and treats a

strongly derived group, the Calliopsini, along with its closest relatives, *Protomeliturga* (Protomeliturgini) and *Perdita* (Perditini). The three tribes are restricted to the Western Hemisphere.

Robertson (1922) recognized Calliopsinae as one of the subfamilies of his Panurgidae but otherwise authors have not recognized a higher taxon based on *Calliopsis*. The Calliopsini, as here understood, contains five genera: *Acamptopoeum*, *Calliopsis* (11 subgenera, two of them new), *Arhysosage*, *Spinoliella* (2 subgenera) and *Callonychium* (2 subgenera). The genus *Calliopsis* is treated here in a wider sense than in the past.

## MATERIALS AND METHODS

About 20,000 panurgine bees have been the study material for this and previous investigations (Ruz, 1986). At least three species (3 individuals each, or more if required) of each polytypic genus and subgenus have been carefully examined and dissected. Structures like male genitalia and associated sterna, sting apparatus of female, mouthparts, last tergum and sterna 5 and 6, were cleared in a cold solution of KOH (10%) for 12 hours or less, depending on the degree of sclerotization of the structures, then washed with water for several minutes and preserved in glycerol for later examination.

The morphological analysis of the species selected as representatives of each genus (type species plus at least two additional species when possible) was made using a stereomicroscope and, for details, a compound microscope. The names of the species studied in detail are preceded with an asterisk (\*) in lists of species under each taxon.

Illustrations were made using a camera lucida,

comparable structures being drawn at about the same size regardless of differences in size of the bees. Sternum 6 of females was drawn with the latero-distal margin in its ordinary, curved position in order to avoid breaking it; therefore the distal part of the sternum appears somewhat narrower than in a flattened sternum. Figures of certain structures are omitted if similar structures are illustrated for related taxa or if other sources with good drawings are available.

In the descriptions, each character (or groups of morphologically associated characters) is numbered. For purposes of comparison these numbers have been maintained within taxa of the same level. Certain characters (and numbers) are omitted if they are similar in related taxa. Subfamilial characters are omitted in the tribal, generic and subgeneric descriptions, unless they represent an exception for the group; in this case those distinctive characters are kept in the description. The number of a given character used in the

descriptions is not coincident with that used for Tables 1 and 2 and the cladogram (Fig. 30).

In order to facilitate comparisons, the number of each apomorphy as it appears in Table 1 and in Ruz (1986) has been maintained for the whole revision of the subfamily. The numbers of the characters not used in the Calliopsini and their close relatives are skipped in the present work. In order to maintain the sequence of numbered apomorphies, certain autapomorphies have been inserted with a number already used plus a letter.

The morphological terms in the descriptions are mainly based on those used by Snodgrass (1935, 1956), Michener (1944, 1965, 1981), Rozen (1951), Winston (1979), and Michener and Brooks (1984). Some characters whose interpretations may be difficult are explained below.

20. Basal area and apex of labrum: As indicated in Figure 1F.
33. Tentorial pit: Small, rounded, the most dorsal part of the external depression associated with the anterior tentorial arms (Fig. 6A, D).
39. Orbits: Inner ocular orbits, as seen in facial view (Fig. 6A-D).
46. Pterostigma and prestigma lengths (Fig. 2E) were measured on vein Rs; their breadths (maximum) were measured perpendicular to the lengths. Prestigma width was not measured to the wing margin but is only the width of the prestigma proper.
48. Submarginal cells (SM): For length comparison, SM cell 2 (if only two SM cells present) has been called SM cell 2 + 3 assum-

ing that vein 1st r-m (2nd transverse cubital vein) has disappeared. When three SM cells are present, cells 2 and 3 are indicated as SM 2 and 3.

50. Cell 2nd M of forewings: 3rd discoidal cell.
69. Male terga: Postgradular depression width measured along the longitudinal axis of the body.
70. Pygidial plate: Glabrous plate on distal part of T7 of male and T6 of female (the latter not considered here), laterally delimited by carinae. The same area delimited only by hairs or only a projection of last tergum has not been considered as a real plate in this study.
71. T7 of female: Hemitergite of Michener, 1944.

In describing margins of a leg segment, the leg has been considered as extended laterally; the antenna has been considered extended forward. The word vertex has been used to mean the posterior margin of the vertex rather than the whole top of the head.

In order to save space, terga and sterna are abbreviated as T or S plus arabic numbers of the metasomal segments (i.e., not counting the propodeum). Thus T1 is the first metasomal (second abdominal) tergum.

#### ACKNOWLEDGMENTS

Acknowledgments for the study material used in the whole revision of the subfamily are given here. They may be omitted in subsequent papers of this series. Abbreviations in parentheses are used for institutions or collections through the rest of the work.

This study would not have been possible without the encouragement and assistance of numerous people. I am particularly grateful to Charles D. Michener of the Department of Entomology, University of Kansas (KU), Lawrence, Kansas, for his generosity, advice, interest and help in the preparation of the manuscript and for the use of material in the Snow Entomological Museum (KU). I also thank the following persons: George W. Byers and the late Peter D. Ashlock (KU) for their suggestions in editing the manuscript; Edward O. Wiley (KU) for his advice and willingness to discuss aspects of this investigation; Frank Koch of the Museum für Naturkunde der Humboldt-Universität, Berlin, for lending Friese's types and other valuable specimens, as well as generously permitting study of material from the collection under his care when I visited the Museum; George R. Else of the British Museum (Natural History), London, England; Till Osten of Staatliches Museum für Naturkunde, Stuttgart, Germany; and Mario Zunino of the Museo ed Istituto di Zoologia Sistemática della Università di Torino, Italy, also kindly lent type specimens. The late Radclyffe B. Roberts of Rutgers University, New Brunswick, New Jersey and John L. Neff of the Central Texas Melittological Institute, Austin (CTMI), lent and donated im-

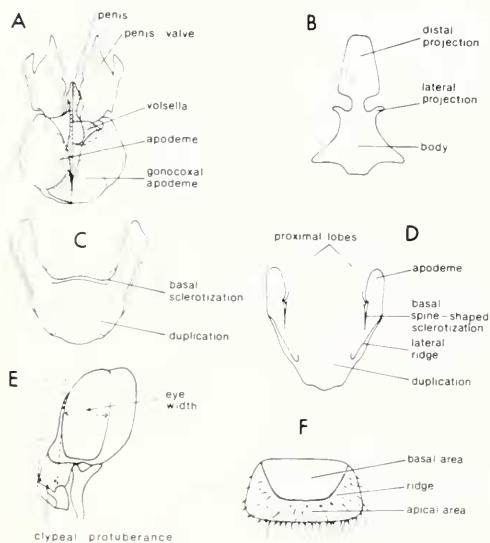


Figure 1. Diagram to show terminology for *Calliopsis* (A, B, D-F) and *Perdita* (C). A, Male genitalia, dorsal and ventral views; B, S8 of male; C, D, S6 of females; E, Head, lateral view; F, Labrum.

portant specimens. Professors Salvador Peris and Elvira Mingo of the Instituto Español de Entomología of Madrid, Spain, permitted my study of that collection. Yu. A. Pesenko of the Zoological Institute, Academy of Sciences, Leningrad; Klaus Warncke of Ruckteschellweg, Germany; George C. Eickwort of the Department of Entomology, Cornell University, Ithaca, New York; the late Robert O. Schuster of the University of California, Davis, California (UCD); Paul H. Arnaud of the California Academy of Science, San Francisco, California; Wallace E. LaBerge, Illinois Natural History Survey, Champaign, Illinois; and William L. Overal of the Museu Paraense Emilio Goeldi, Belém, Pará, Brazil, lent important study material. Ronald J. McGinley of the Smithsonian Institution, Washington, provided material from the Reed Collection then under his care at Harvard University, Cambridge, Massachusetts (MCZ). Robert W. Brooks of the Snow Entomological Museum, University of Kansas, Lawrence, Kansas (KU), helped in the preparation of diagrams, made some preliminary photographs and provided certain specimens for study. Terry Griswold of the U.S. Department of Agriculture, ARS-Bee Laboratory, Utah State University, Logan, Utah (USDA), lent study material, made available the panurgine collection of the Bee Laboratory and kindly provided housing on my visits to Logan. Jerome G. Rozen Jr. of the American Museum of Natural History, New York (AMNH), contributed valuable ideas, lent many specimens for study, permitted the use of the bee collection of the Museum, and very kindly provided housing and help when I visited the Museum. Zine Ajmal de Toledo of the Instituto de Zoología Miguel Lillo, Tucumán, Argentina (IZML), lent an important panurgine collection under her care. Haroldo Toro of the Universidad Católica de Valparaíso, Chile (UCV), made valuable suggestions and provided numerous specimens. Dr. James S. Ashe (KU) and Francisco Saiz (UCV) provided help and let me use photographic equipment under their care; Carlos González (UCV), Chile, and Stephen Reyes (KU) did some photographic work.

I am also indebted to Rudolf Jander, Hans-

Peter Schultze and Arturo Roig-Alsina (all from KU) for their help in translating materials from German to English.

The drawings were mostly inked by Donna Stevens (KU); some of them were also prepared by Carmen Tobar (UCV).

The typing of the manuscript and editorial assistance was by Joetta Weaver (KU). Many thanks also to Virginia Ashlock (KU) for her help in typing and editorial work.

This study was possible thanks to the financial aid of the Dirección General de Investigaciones, Universidad Católica de Valparaíso, Chile, and especially the National Science Foundation grants DEB82-12223 and BSR87-16817 (C. D. Michener, principal investigator).

SUBFAMILY PANURGINAE

*Diagnosis.* Short-tongued bees usually with non-metallic integument, 2-11 mm long; first segment of labial palp usually flattened; labrum (proximally) without lateral process to articulate with clypeus as in Andreninae; paraglossa elongate and somewhat tapered distally, usually as long as suspensorium or longer (in Andreninae wider distally and shorter than suspensorium); scrobal suture usually absent; marginal cell distally truncate (often obliquely); middle femur of female with ventral margin a ridge, with a comb basally and sparse plumose hairs distally; scopa present, mainly on tibia and basitarsus, moderately abundant to sparse; T2 with lateral fovea or at least a dark spot; gonobase absent (except 3 genera with a "gonobase" that may not be homologous with the real gonobase).

The three panurgine tribes considered in the present paper, Perditini, Protomeliturgini and Calliopsini, share the following principal characters: 47. Submarginal cells two (exceptionally three in Perditini). 66. Tibial scopa of female usually (at least partially) of minutely branched hairs. 82. Gonocoxal apodeme not inflexed. 88. Sting short to extremely short, with first valvula slightly sclerotized, without valve (except a possible rudiment in *Calliopsis (Ceroliopoeum)*).

KEY TO TRIBES CALLIOPSINI, PROTOMELITURGINI AND PERDITINI

- 1. Marginal cell (nearly always) about half as long as distance between its apex and wing tip (Fig. 2B); if longer, then lower part of face, in profile, not or scarcely divergent from eye. S6 of male 3 or more times as broad as long (length measured medially); distal margin medially almost straight or with very wide and rather shallow V-shaped emargination. Usually with metallic color . . . . . Perditini
- Marginal cell more than half as long as distance between its apex and wing tip. Lower part of face, in profile, distinctly divergent from eye. S6 of male usually less than 3 times wider than long; if wider, then distal margin with tapered projections and rather deeply emarginate medially; or if otherwise, of different shape than above. Almost never metallic . . . . . 2
- 2. Tentorial pit at intersection of outer subantennal and epistomal sutures. Pre-episternal groove extending below scrobal level. Middle femur of female with hairs of ventral margin not well organized in a comb . . . . . Protomeliturgini

—Tentorial pit in outer subantennal suture (Fig. 6A–D). Pre-episternal groove short, absent below scrobal level. Middle femur of female with a distinct, well-defined comb basally on ventral margin (Fig. 10D). . . . . Calliopsini

### TRIBE PERDITINI

This tribe contains a single enormous genus, restricted to North America. It has not been reclassified in the present work; it is diverse but monophyletic. In the current classification it contains only the genus *Perdita*, which is subdivided into 21 subgenera.

The following features characterize this tribe: 2. Integument usually metallic and with yellow markings. 33. Tentorial pit usually at intersection

of outer subantennal and epistomal sutures. 45. Pre-episternal groove curved, meeting scrobe. 46. Pterostigma large, with sides divergent; margin within marginal cell clearly convex. 47. Marginal cell usually half as long as distance between its apex and wing tip or less. 61. Hind tibia of male with dorsal border usually untoothed. 69. T2–5 of male with posterior marginal areas glabrous or nearly so. 72. T8 of male usually tapered distally and hairy. 76. S5 of female with distal margin broadly concave. 77. S6 of male about three times as broad as long (length measured on midline). 82. Gonocoxal apodeme not inflexed. 83. Gonocoxites fused ventrally. 85. Volsellae weakly attached to each other medially, with denticles. 88. Sting extremely short, rudimentary, second valvifer elongate, first valvula slightly sclerotized, without valve.

### Genus *Perdita* Smith

(Figs. 2, 3, 30)

*Perdita* Smith, 1853: 128. Type species: *Perdita halictoides* Smith (monobasic).

The list of subgenera and synonymy for each can be found in Hurd (1979), with another subgenus in Timberlake (1954).

I have not attempted to study the subgenera (or genera?) encompassed under the name *Perdita*. In the following description, however, I have attempted to indicate the variation within *Perdita* in characters useful elsewhere at the generic level. To shorten the description I use mostly subgeneric names to identify variants; in reality, however, I have examined primarily the species listed below and the use of a subgeneric name does not indicate that all species of that subgenus have the specified characters: *Perdita* s. str. (*halictoides* Smith); *Pentaperdita* (*albovittata* Cockerell); *Perditella* (*larreae* Cockerell); *Hexaperdita* (*ignota crawfordi* Cockerell); *Pygoperdita* (*interrupta* Cresson); *Heteroperdita* (*trifasciata* Timberlake, female); *Glossoperdita* [*pelargoides* (Cockerell)]; *Hesperoperdita* (*trisignata* Cockerell); *Alloperdita* (*novaeangliae* Viereck, female); *Macrotera* [*texana* (Cresson), *bicolor* Smith]; *Macroterella* (*mortuaria* Timberlake, male); *Macroteropsis* (*latior* Cockerell); *Pseudomacrotera* (*turgiceps* Timberlake); *Allomacrotera* (*stephanomeriae* Timberlake, male); *Epimacrotera* (*ainsliei* Crawford); *Callomacrotera* (*maritima* Timberlake, *acapulcona* Timberlake); *Cockerellia* (*albipennis* Cresson); *Cockerellula* (*opuntiae* Cockerell); *Procockerellia* (*albonotata* Timberlake); *Xerophasma* (*bequaertiana* Cockerell). Additional information on characters and their variability among and within subgenera of *Perdita* is given by Ruz (1986) and Danforth (1991).

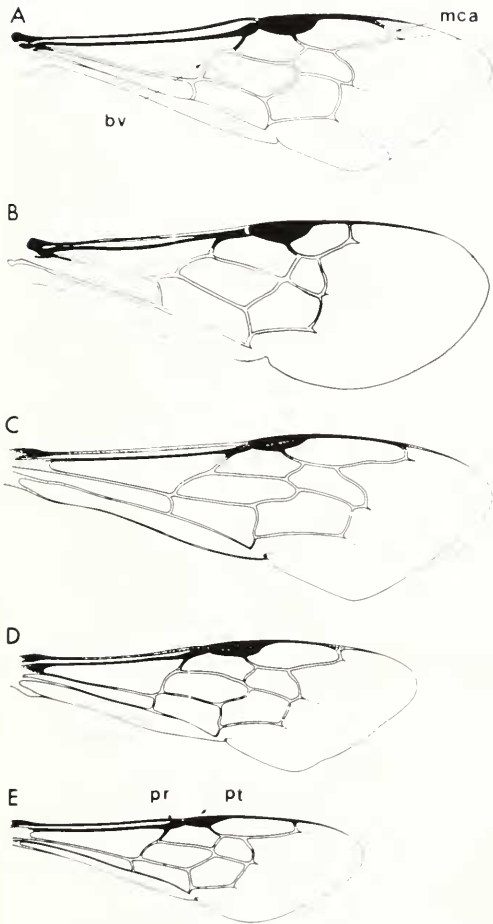


Figure 2, A–E. Forewings of males. A, *Protomeliturga turnerae* (Ducke); B, *Perdita halictoides* Smith; C, *Acamptopoeum submetallicum* (Spinola); D, *Calliopsis* (*Ceroliopoeum*) *laetum* (Vachal); E, *Calliopsis* (*Hypomacrotera*) *callops* (Cockerell and Porter). pt = pterostigma; pr = prestigma; mca = marginal cell apex; bv = basal vein.

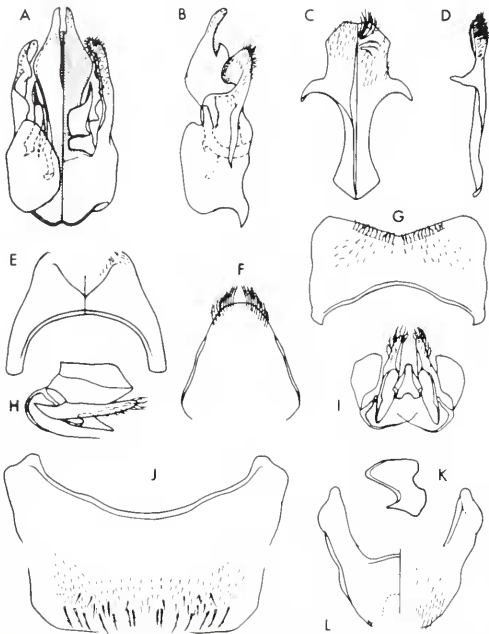


Figure 3. *Perdita halictoides* Smith. Male: A, B, Genitalia, dorsal, ventral and lateral views; C, D, S8, dorsal, ventral and lateral views; E, S7, dorsal and ventral views; F, T8; G, S6, ventral view. Female: H, Sting; I, Sting, ventral view; J, S5, ventral view; K, T7; L, S6, dorsal and ventral views.

*Description.* 1. Length 2–11 mm. 2. Integument metallic (at least partially), except in species of the subgenera *Macrotera*, *Macroterella*, *Xerophasma*, *Perditella*, *Cockerellula*. 5. Pubescence in general short, usually minute on most of metasoma, especially on terga. 8. Head narrower to wider than thorax. 11. Glossa much shorter to longer than prementum; usually with flabellum. 17. Galeal comb of 0–15 setae. 20. Labrum less than twice as broad as long to more than twice as long; basal area usually glabrous, sometimes almost fully pilose; distal margin of basal area a ridge; labrum somewhat protuberant, with apex inflexed or not. 25. Mandible of male simple to bidentate, or with prebasal tooth-like projection. 30. Inner subantennal suture usually curved, sometimes almost straight. 33. Tentorial pit usually at intersection of outer subantennal and epistomal sutures (sometimes in outer suture though close to the epistomal suture). 34. Antennal sockets below middle of face [e.g., *P. (P.) halictoides* Smith] to slightly above as in *Xerophasma*. 36. Antennal flagellum of male unmodified, shorter to longer than head. 37. Lower mesal paraocular area rather flattened or slightly convex as in *P. (P.) halictoides* (sometimes somewhat protuberant). 39. Orbits usually subparallel, sometimes convergent below as in

*Callomacrotera*, or divergent below as in male of *Macrotera*. 45. Pre-episternal groove usually curved, reaching scrobe, sometimes absent (e.g., *Macrotera*, *Macroteropsis*, *Cockerellia*, *Pentaperdita*). 46. Pterostigma longer than and twice as broad (or more) as prestigma; margin basal to vein r clearly diverging from costa (slightly so in *Macrotera* and *Macroteropsis*); margin within marginal cell usually convex [except in *Macrotera* and in *P. (Macroteropsis) latior*]. 47. Marginal cell broadly truncate, very short, usually nearly half as long as distance from apex to wing tip (Fig. 2B) (not as short in *Xerophasma* and *Macrotera*). 48. Submarginal cells two except in *Xerophasma* and *Alloperdita*, which have three, but second small and petiolate anteriorly. 50. Cell second M sometimes absent or weak. 51. First recurrent vein usually close to first transverse cubital, sometimes meeting it. 55. Propodeal triangle with no visible hairs (sometimes with sparse, minute hairs [e.g., *P. (Allomacrotera) stephanomeriae*, *Epimacrotera ainsliei*, and *P. (Glossoperdita) pelargoides*]). 57. Basitarsus 1 (both sexes) from six to nine times longer than broad; tarsomeres 2–4 unmodified. 58. Femur 2 of female with comb on ventral margin basally not well defined (not easily differentiated from other hairs). 59. Middle tibial spurs finely toothed, slightly curved (or almost straight), somewhat shorter than basitarsus 2; strongly curved at apex in *Macrotera*. 61. Tibia 3 of female somewhat less than twice as long as basitarsus 3, with keirotichia on most of inner surface, sometimes very sparse toward the middle, only at ends, or apparently absent; male with dorsal margin of tibia 3 usually untoothed, with keirotichia usually on most of surface, sometimes sparse. 62. Tibial scopa usually of rather short hairs (long in some species); in most cases apparently simple but with minute branches, with rather long alternate branches in *P. (Callomacrotera) maritima* Timberlake; scopal hairs usually sparse or moderately abundant, dense in *Macrotera* and *Callomacrotera*. 63. Hind tibial spurs usually slightly curved, strongly curved at apices as in *Macrotera*; outer spur usually shorter than inner. 64. Basitibial plate of male well defined. 66. Claws bifurcate. 67. Metasoma in male usually wider than to sometimes narrower than thorax. 70. Pygidial plate of male absent, though T7 at apex usually with median projection (projecting area truncate, bifurcate, or tapered). 71. T7 of female as in Figure 3K. 72. T8 of male generally somewhat tapered at apex, distinctly hairy (Fig. 3F). 74. S4 of male with distal margin broadly and gently concave or almost straight. 75. S5 of male with distal margin widely and gently concave (sometimes almost straight). 76. S5 of female with no median sclerotized area proximally and no gradulus; distal margin broadly and shallowly concave (Fig. 3J). 77. S6 of male three or more times wider than long (length measured medially), distally with a very wide V-shaped emargination or margin almost straight (Fig. 3G). 78. S6 of female with no proximal laminar lobes, basal

sclerotization fully fused to sternum and not spine-shaped (similar to that of *Protomeliturga*), lateral margin with ridge almost straight or curved, longitudinal basal carina absent, duplication membranous (sclerotized area below it), distal margin distinctly concave or narrowly emarginate medially, S6 with small sparse hairs proximally, forming dense patch at both sides of midline distally (Figs. 1C, 3L). 79. S7 of male with two distal lateral lobes and with shallow to deep V-shaped or concave apical emargination (Fig. 3E). 80. S8 of male cross-like with distal part wide to narrow, truncate, rounded or tapered; basal part wider to narrower than distal projection (Fig. 3C, D), bilobed, or bifurcate in some species. 82. Gonocoxal apodeme well or usually strongly developed (laterally or medially in ventral view), not inflexed (Fig. 3A, B). 83. Gonocoxites elongate, connected by slightly sclerotized cuticle to fully fused ventrally. 84. Gonostylus fused to gonocoxite, well developed, elongate. 85. Volsellae attached to each other by small membranous area; with denticles. 86. Penis valves elongate, simple, usually tapered apically, fused to each other generally rather extensively (sometimes free only at apices). 87. Penis membranous, usually almost as long as and wider than valve, fused to valves in great part. 88. Sting short (sometimes truncate, e.g., *P. halictoides*), not reaching stylus, first valvifer (triangular plate) rather elongated (not triangular), first valvula little sclerotized, valve absent (Fig. 3H, I).

**Comments.** This is the largest genus of the subfamily, containing approximately 500 species, grouped in 21 subgenera and several species groups.

**Discussion.** The genus *Perdita*, in spite of all the diversity that it presents, has several apomorphies that make it a distinctive group. According to the cladogram (Fig. 30) this genus is the sister group of the Calliopsini and *Protomeliturga* together. Rozen (1966) has found that *Perdita* has distinct larval characters different from those of any other Panurginae.

The pollen balls in the cells of several species of *Perdita* are coated with a secreted, cellophane-like layer, a synapomorphy shared with the Calliopsini (Rozen, 1967, and personal communication). If *Protomeliturga* does not cover the pollen ball, this fact may mean that *Perdita*, not *Protomeliturga*, is the sister group of Calliopsini. This was the result that I obtained in a preliminary cladistic analysis using a smaller set of characters.

**Distribution.** This genus occurs in southern Canada, the United States, México and Guatemala (Hurd, 1979).

#### TRIBE PROTOMELITURGINI

The main characters of this monotypic tribe are the following: 20. Labrum of female with

basal area hairy laterally. 33. Tentorial pit at intersection of outer subantennal and epistomal sutures. 45. Pre-episternal groove extending below scrobal level. 46. Pterostigma with sides diverging; margin within marginal cell convex. 61. Hind tibia of male with dorsal border a carina. 69. T2-5 of male with posterior marginal areas pilose laterally forming a hair band. 70. T7 of male with a strong lateral projection. 76. S5 of female with distal margin almost straight. 82. Gonocoxal apodeme not inflexed. 83. Gonocoxites short, fused ventrally. 85. Volsellae well separate from each other, without denticles. 87. Penis extremely wide and completely fused to penis valves. 88. Sting very short, first valvula little sclerotized, without valve.

#### Genus *Protomeliturga* Ducke (Figs. 2A, 4, 5, 30)

*Protomeliturga* Ducke, 1912: 63, 90. Type species: *Calliopsis turnerae* Ducke, 1907 (monobasic).

**Diagnosis.** Segments 3 and 4 of labial palp at right angle to segment 2. Basal vein (forewing) strongly curved. Terga with distal hair bands laterally. **Male.** Antennal flagellum much shorter than length of head. Tibia 3 with dorsal margin a sharp carina. T7 at apex strongly bent down and forward, with a conspicuous projection laterally.

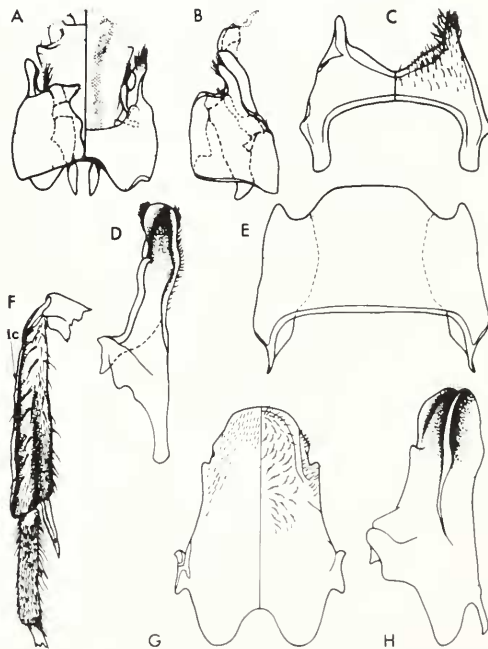


Figure 4. *Protomeliturga turnerae* (Ducke). **Male:** A, B, Genitalia, dorsal, ventral and lateral views; C, S7, dorsal and ventral views; D, S8, lateral view; E, T7; F, Leg 3, outer view; G, S8, dorsal and ventral views; H, S8, ventrolateral view. tc = tibial carina.

*Female.* Middle tibial spur finely and densely toothed. Tibia 3 more than twice as long as basitarsus 3, with scopae mostly of long, minutely branched hairs. Inner hind tibial spur conspicuously curved.

*Description.* 1. Length 5–8 mm. 3. Lower part of face (clypeus of male, small spot in lower paraocular of female) and areas of thorax and legs yellow. 4. Metasoma with no yellow marks. 5. Pubescence in general short, mostly appressed, rather abundant, inconspicuous in most of dorsum of thorax. 6. Integument microareolate, dull on most of head and thorax, shiny on metasoma. 7. Punctures fine, mostly dense. 8. Head wider than long and narrower than thorax (sometimes as broad as thorax). 11. Glossa somewhat longer than prementum. 13. Segment 1 of labial palp longer than 2–4 together. 14. Segment 2 of labial palp about three times longer than 3. 15. Segment 3 of labial palp articulated at angle to segment 2 so that 3 and 4 project at angle to 1 and 2 (as in long-tongued bees). 16. Maxillary blade more than twice as long as prepupal part of galea. 17. Galeal comb of about 11 bristles. 20. Labrum somewhat wider than long; basal area densely hairy and with distal margin a strongly projecting ridge; labral apex strongly inflexed as in *Pseudopanurgus* (Fig. 5B, C). 27. Clypeus slightly more than twice as wide as long in male, a little less than three times in female; moderately protuberant (about 1/3 width of eye in lateral view); distal margin with rounded projection near lateral margin of labrum (Fig. 5I, K, L). 30. Inner subantennal suture almost straight. 31. Subantennal area wider than half length of inner suture and as wide as socket. 33. Tentorial pit at intersection of epistomal and outer subantennal sutures (Fig. 5I). 34. Antennal sockets in middle of face. 36. Flagellum of male slightly clavate (Fig. 5J), much shorter than head; flagellomere 1 about twice as long as 2, longer than broad. 37. Lower mesal paraocular area slightly convex. 38. Facial fovea narrow and shallow in male, wider and well-marked in female. 39. Orbits convergent below in male, subparallel in female. 40. Ocelli mostly above orbital tangent. 41. Vertex convex. 42. Gena of male (lateral view) narrower than eye, of rather uniform width. 43. Pronotum with dorsolateral preapical lamella, without dorsal ridge medially. 44. Mesepisternum with almost no flat area facing anteriorly. 45. Pre-episternal groove rather shallow, punctate, extending below scrobe, more clearly marked above. 46. Pterostigma longer and wider than prestigma; side basal to vein r clearly diverging from costa, that within marginal cell convex. 47. Marginal cell rather pointed at apex (obliquely truncate, Fig. 2A); length little shorter to somewhat longer than distance from its apex to wing tip. 48. Submarginal cells two. 49. Submarginal cell 1 about as long as cell 2 + 3. 50a. Basal vein strongly curved. 51. First recurrent vein distant from first transverse cubital. 52. Forewing with cu-v longer than second abscissa of M + Cu. 53. Hind wing with

cu-v 1/4 to 1/5 as long as second abscissa of M + Cu. 54. Dorsal surface of propodeum about as long as metanotum. 55. Propodeal triangle densely pilose, especially on lateral areas, with no striae. 57. Basitarsus 1 about six times longer than broad in male and more than three times longer in female; tarsomeres 2–4 unmodified. 58. Femur 2 of female on ventral margin basally with comb not well developed and not clearly defined. 59. Middle tibial spur of both sexes slightly more than half as long as basitarsus 2 with fine, minute and dense teeth. 60. Basitarsus 2 of both sexes about as long as 1 and shorter than 3. 61. Tibia 3 of female more than twice as long as basitarsus 3 (Fig. 5H), with keirottrichia on most of inner surface except close to dorsal and ventral margins; male tibia 3 with dorsal margin a strong, sharp carina (as in *Pseudopanurgus*) (Fig. 4F), with keirottrichia as in female. 62. Tibial scopae mostly of long, branched hairs (some with branches only distally, a few on dorsal margin simple). 63. Hind tibial spurs with minute, fine teeth; outer somewhat shorter than inner and slightly curved at

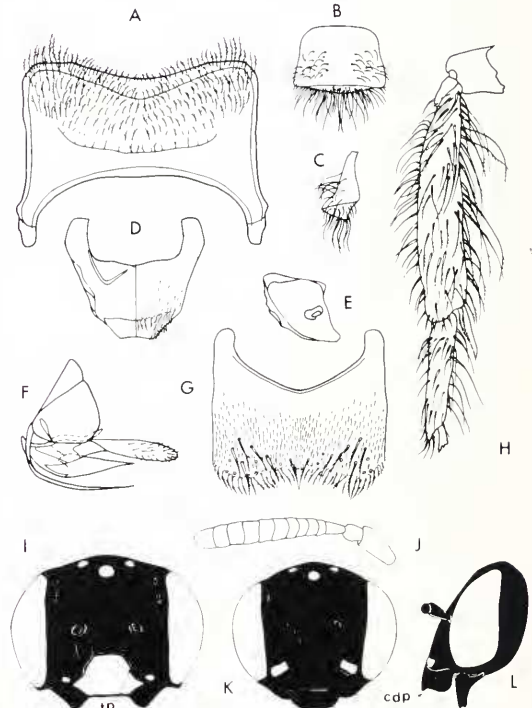


Figure 5. *Protomeliturga turnerae* (Ducke). *Male*: A, S6, ventral view. *Female*: B, Labrum; C, Labrum, lateral view; D, S6, dorsal and ventral views; E, T7; F, Sting; G, S5, ventral view; H, Leg 3, outer view; I, Head, frontal view (hairs and labrum omitted). *Male*: J, Antenna; K, L, Head, frontal and lateral views (hairs omitted, labrum only in K). tp = tentorial pit; cdp = distal clypeal projection.



apex; inner more conspicuously curved, especially in female. 64. Basitibial plate of male well defined, margins carinate. 65. Tarsus 3 with no modifications except basitarsus of female with small apical projection. 66. Claws deeply cleft; rami subequal in male, inner shorter than outer in female. 67. Metasoma in male somewhat broader than thorax. 69. T2-5 of male with gradulus posterolaterally absent and with postgradular depression rather shallow; posterior marginal areas of T1-5 in male and T1-4 in female pilose, forming bands laterally (band less distinct on T5 of male and T4 of female); lateral fovea of T2 (both sexes) rather narrow, gently depressed. 70. Pygidial plate of male absent; T7 at apex strongly curved down and forward, with a conspicuous projection laterally (Fig. 4E). 71. T7 of female as in Figure 5E. 72. T8 of male trapezoidal. 73. Metasomal sterna of male mostly with hairs straight, short, appressed, except on S6 obliquely directed toward midline. 73a. S1-5 of female with hairs as in male but longer and branched on premarginal areas. 74. S4 of male with distal margin slightly and broadly convex. 75. S5 of male with margin straight medially. 76. S5 of female with neither median proximal sclerotized area nor gradulus; distal margin broadly and gently concave (Fig. 5G). 77. S6 of male broadly and gently concave medially (Fig. 5A). 78. S6 of female similar to that of *Pseudopanurgus* except longitudinal basal carina absent; duplication well sclerotized; distal margin slightly concave medially; premarginal area fully hairy but sparsely so medially; rest of sternum with hairs minute (Fig. 5D). 79. S7 of male wide, distally with a V-shaped emargination and a lateral, short projection; proximal arms forming a U (Fig. 4C). 80. S8 of male wide, large, strongly carinate laterally and much exposed distally (surpassing T7) (Fig. 4D, G, H). 82. Gonocoxal apodeme well developed (dorsal view), rather wide, not inflexed (suture almost invisible) (Fig. 4A, B). 83. Gonocoxites much shorter than penis valve, fused medially. 84. Gonostylus fused to gonocoxite, slightly shorter than half length of gonocoxite. 85. Volsella strongly lateral in position, free mesally, fused to gonocoxite proximally, without denticles. 86. Penis valves wide, completely fused to each other and to penis. 87. Penis long (slightly surpassing penis valve), extremely wide, with two mesal longitudinal sclerotized areas. 88. Sting short, not reaching stylus, first valvula little sclerotized, valve absent (Fig. 5F).

*Comments.* This genus is known only from one species, *Protomeliturga turnerae* (Ducke).

The material available for this study was: the type of *P. turnerae* (lectotype female and lectoallotype male) from the Museu Paraense Emilio Goeldi (Belém, Pará, Brazil) (not dissected) and two specimens (one male and one female) from the Berlin Museum which, although labeled "Typus," are not the real types. The specimens

from the two museums are certainly conspecific.

*Discussion.* The cladistic analysis shows this species to be the sister group of the Calliopsini. It presents a series of derived features, although at first sight the genus suggests a rather primitive panurgine. Probably because of its lateral hair bands on the metasomal terga, Ducke (1907) erroneously placed it in *Calliopsis*.

*Distribution.* *Protomeliturga* is known only from São Luiz de Maranhão, Brazil.

#### TRIBE CALLIOPSINI

This tribe, found only in the western hemisphere, is the most derived group of the Panurginae. I list below a series of its characters, using the same series of character numbers as in the generic descriptions, in order to avoid repetition in the descriptions of the genera as well as to emphasize the unity of the tribe.

30. Inner subantennal suture about as long as antennal socket diameter or shorter. 33. Tentorial pit in outer subantennal suture. 45. Pre-episternal groove rather short, absent below scrobal level. 46. Pterostigma basally nearly as wide as distally or little narrower; side within marginal cell usually straight. 48. Submarginal cells two. 55. Propodeal triangle glabrous. 58. Middle femur of female, on ventral margin, with a distinct, well-defined comb. 61. Tibia 3 of female, on inner surface, with keitrichia present toward dorsal border and at base and apex, sometimes only at the two ends; male tibia 3 with dorsal border untoothed. 62. Tibial scopa, on outer surface, of sparse to extremely sparse, mostly minutely branched and simple hairs. 69. T1-5 of male and T1-4 of female with posterior marginal area usually completely or partially hairy (short hairs). 70. Pygidial plate of male usually present. 72. Tergum (T)8 of male usually about as wide as long and roughly hexagonal but with lateral angles rather rounded. 73. S1-5 of male with hairs mostly directed straight backward. 76. S5 of female with a median sclerotized area between proximal margin and gradulus except in *Callonychium* (Fig. 10E); gradulus usually short except in *Callonychium* long and recurved; distal margin broadly convex medially. 78. S6 of female with proximal laminar lobes; with basal spine-like sclerotization except of different shape in some *Calliopsis* (*Nomadopsis*) and absent in *Callonychium*; basal sclerotization free from disc of sternum distally (except fused on *Arhysosage*); lateral margin with a strong, usually almost straight ridge; longitudinal basal carina absent; duplication usually at least somewhat sclerotized except thin in some *Calliopsis* s. l.; most of surface with minute sparse hairs except apically with well-defined rows of dense hairs forming a lateral patch or a continuous, usually curved, band of hairs. 80. S8 of male with distal projection well developed;

basal body with a lateral acute projection except in *Acamptopoeum* and *Calliopsis* (*Verbenapis*), which have no projection or only a small convexity, respectively. 82. Gonocoxal apodeme (ventral view) conspicuous, not inflexed. 83. Gonocoxites globose, connected with one another by weakly sclerotized cuticle to completely fused and highly sclerotized. 84. Gonostylus inconspicuous or absent. 85. Volsella usually well developed and without denticles [except with denticles in *C. (Nomadopsis)*]; volsella sometimes apparently absent or rudimentary (completely fused to gonocoxite?) as in *Arhysosage*, *Spinoliella* and *Callonychium*. 86. Penis valves dorsally fused through a small, narrow bridge. 88. Sting usually short or greatly reduced (except surpassing stylus in *Acamptopoeum*); second valvifer (triangular plate) usually unmodified; first valvula only slightly

sclerotized, valve absent [except a rudiment of valve in *Calliopsis* (*Ceroliopoeum*)].

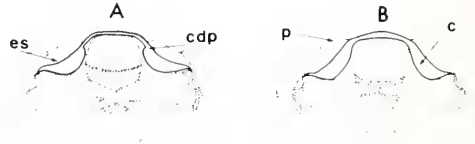


Figure 7. A, B. Heads of males, ventral views. A, *Spinoliella (Peniella) maculata* (Spinola); B, *Callonychium (Callonychium) mandibulare* Brèthes. cdp = distal clypeal projection; es = epistomal suture; c = clypeus, lateral area; p = paraocular area.

KEY TO THE GENERA OF THE TRIBE CALLIOPSINI

- 1. Male ..... 2
- Female ..... 6
- 2. Orbits convergent below. Tentorial pit clearly below median point of outer subantennal suture (Fig. 6A, B) ..... 3

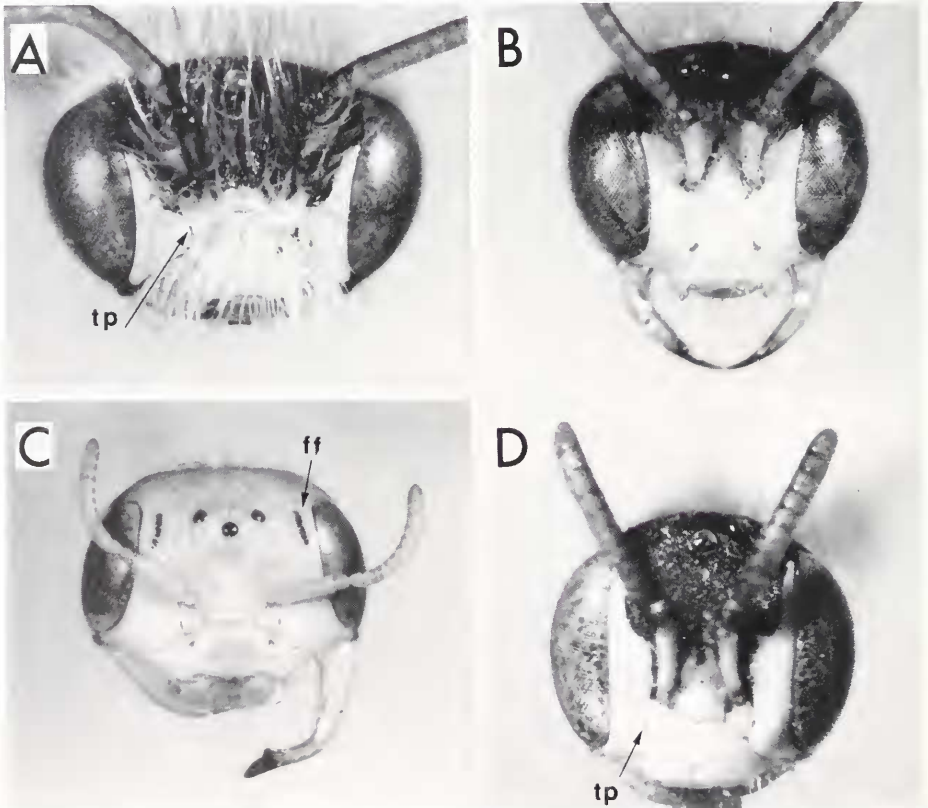


Figure 6. A-D. Heads of males, frontal views. A, *Acamptopoeum submetallicum* (Spinola); B, *Calliopsis (Calliopsis) andreniformis* Smith; C, *Arhysosage ochracea* Brèthes; D, *Callonychium (Paranychium) chilense* (Friese). tp = tentorial pit; ff = facial fovea.

- Orbits subparallel or divergent below. Tentorial pit at median point of outer subantennal suture or nearly so (Fig. 6C, D). . . . . 4
3. T7 distally with a median smooth area, delimited by hairs, tapered at apex. S4 with distal margin straight medially. S5 on distal margin without median projection or any other modification . . . . . *Acamptopoeum*
- T7 with pygidial plate rounded or truncate at apex (sometimes poorly delimited by ridge or carina laterally). S4 with distal margin usually produced in middle, broadly concave mesally (Fig. 11G). S5 with well-developed median projection on distal margin, though sometimes inconspicuous (Figs. 11C, 18E, 20H). . . . . *Calliopsis*
4. Orbits strongly divergent below. Lower paraocular area flat. Most of body yellow. Hind tibial spurs strongly curved (similar to those of female in Fig. 26C). Metasoma much wider than head. Total length about 1 cm or nearly so . . . . . *Arhysosage*
- Orbits usually subparallel, if not so, lower paraocular area very swollen on inner area. Body with yellow markings but usually predominantly black. Inner hind tibial spur almost straight, outer straight or somewhat curved (similar to those of female in Fig. 27G). Metasoma as broad as head. Total length 4–7 mm . . . . . 5
5. Metasoma at apex slightly curved or straight. Paraocular area yellow only on lower part. Clypeus (ventral view) distally with projection beside lateral part of labrum; epistomal suture laterally sinuous (Fig. 7A). Antennal socket usually at lower 1/3 of face. . . . . *Spinoliella*
- Metasoma at apex strongly curved downward and forward. Paraocular area with yellow surpassing antennal socket level, usually narrowly following orbit. Clypeus (ventral view) with margins of lateral areas usually almost straight (Fig. 7B). Antennal socket (lower margins) usually at lower 1/4 of face . . . . . *Callonychium*
6. Labrum with basal area well excavated, distal part convex, protuberant in lateral view. Orbits generally convergent below or if not, lower paraocular area not swollen on inner corner . . . . . 7
- Labrum flat or with smooth, rounded, nearly transverse ridge, distal area flat, not inflexed. Orbits subparallel or divergent below . . . . . 8
7. Labrum with basal area at least laterally pilose (Fig. 9F, G). Hind tibia with keirotrichia widespread on most of inner surface (Fig. 10F). . . . . *Acamptopoeum*
- Labrum with basal area usually glabrous; if pilose, also flat (without ridge). Hind tibia with keirotrichia widespread but absent toward ventral margin to completely absent between dense patch at each end . . . . . *Calliopsis*
8. Orbits divergent below. Metasoma wider than thorax. Middle and hind tibial spurs strongly curved at apices (Fig. 26C). Lower paraocular area convex . . . . . *Arhysosage*
- Orbits subparallel. Metasoma about as wide as thorax or narrower. Middle and hind tibial spurs slightly curved (Fig. 27G). Lower paraocular area strongly convex only on inner corner (Fig. 7A, B) . . . . . 9
9. Gena black. Paraocular area on lower part with yellow spot not narrowed along orbit. Antennal sockets at lower 1/3 of face. Claws bifurcate. Facial fovea not linear. . . . . *Spinoliella*
- Gena with longitudinal yellow band to completely yellow (Fig. 8D). Paraocular area with lower yellow spot narrowed along orbit (Fig. 6D). Antennal sockets (lower margins) usually at lower 1/4 of face. Claws simple. Facial fovea linear . . . . . *Callonychium*

### Genus *Acamptopoeum* Cockerell

(Figs. 2C, 6A, 9, 10, 30)

*Friesea* Schrottky, 1902: 418 (preoccupied). Type species: *Friesea brasiliensis* Schrottky, 1902 = *Acamptopoeum prinii* (Holmberg, 1884) (monobasic).

*Acamptopoeum* Cockerell, 1905: 320. Type species: *Camp-topoeum trifasciatum* Spinola, 1851, sensu Cockerell, 1905 = *Acamptopoeum submetallicum* (Spinola, 1851) (monobasic and original designation).

*Parafriesea* Schrottky, 1906: 118 (new name for *Friesea* Schrottky). Type species: *Friesea brasiliensis* Schrottky, 1902 = *Acamptopoeum prinii* (Holmberg, 1884) (autobasic).

*Diagnosis.* Close to *Calliopsis*; distinguishing

characters are as follows: Pubescence of thorax similar in length and density to that of *Colletes*. Orbits convergent below. Labrum with strong transverse salient. Hair bands (sometimes absent in male) on premarginal areas of metasomal terga. *Male.* S4 and S5 with distal margins almost straight. *Female.* Middle tibial spur coarsely toothed. Sting surpassing stylus, truncate at apex.

*Description.* 1. Length 8–11 mm. 2. Integument dull or metallic. 3. Lower half of face (extending up beside orbit), pronotum (sometimes) and legs yellow (spots reduced in female). 4. Metasoma

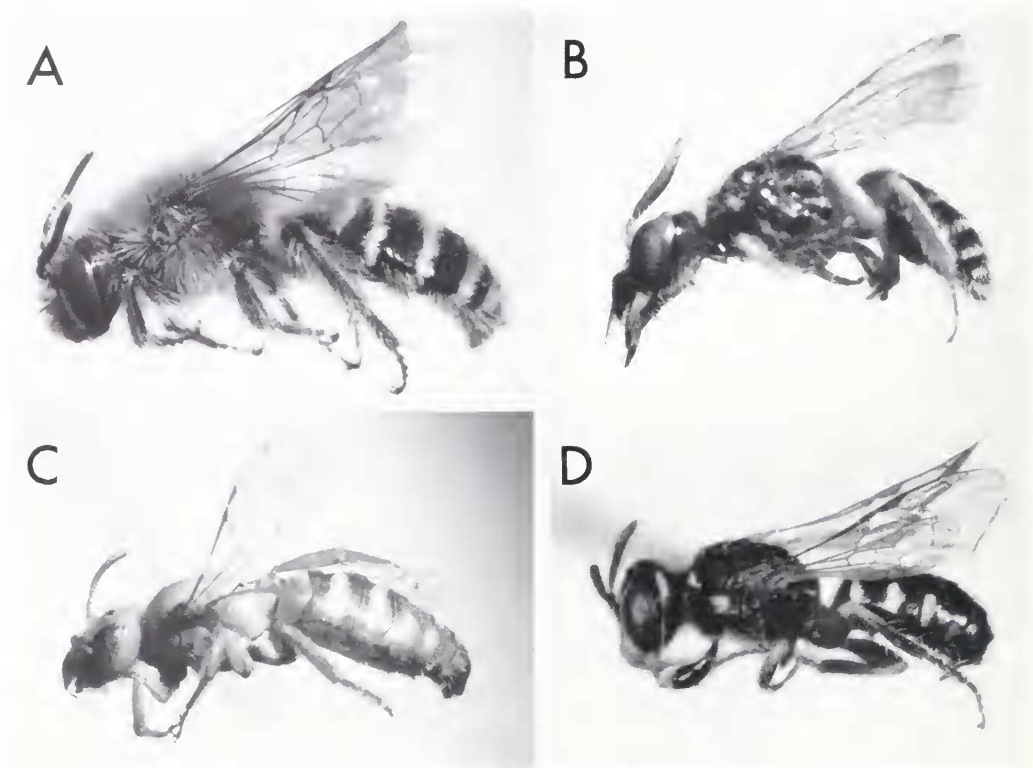


Figure 8, A-D. Calliopsine males, lateral views. A, *Acamptopoeum submetallicum* (Spinola); B, *Calliopsis (Calliopsis) andreniformis* Smith; C, *Arthysosage ochracea* Brèthes; D, *Callonychium (Paranychium) chilense* (Friese).

with no yellow marks. 5. Pubescence relatively long on head and thorax, denser on thorax (similar to that of *Colletes*), much shorter on metasoma. 7. Punctures in general fine, usually dense on thorax and metasoma, sparser on sterna of male. 8. Head distinctly broader than long and broader than thorax. 11. Glossa less than half as long as prementum, slender. 13. Segment 1 of labial palp almost twice as long as 2-4 together or somewhat longer. 16. Maxillary blade less than twice as long as prepalpal part of galea. 17. Galeal comb of 18-24 bristles. 20. Labrum less than twice as broad as long; basal part partially or almost completely pilose; distal margin of basal area strongly salient, hiding inflexed apical part of labrum (Fig. 9F, G). 25. Mandible with upper margin rather conspicuously medially produced. 27. Clypeus somewhat less than three times broader than long and somewhat protuberant (about 1/3 width of eye in lateral view); distal margin with a usually conspicuous acute or rounded projection near lateral margin of labrum. 30. Inner subantennal suture angulate. 31. Subantennal area wider than inner suture length

and than socket. 33. Tentorial pit in outer subantennal suture, but close to epistomal suture. 34. Antennal sockets approximately at middle of face. 36. Antennal flagellum of male unmodified, somewhat longer than head; flagellomere 1 about as long as 2 and about as long as broad. 37. Lower mesal paraocular area rather flattened or slightly convex. 38. Facial fovea oval, shallow. 39. Orbits strongly convergent below. 40. Ocelli above dorsal orbital tangent. 41. Vertex convex. 42. Gena of male (lateral view) somewhat variable (usually narrower than eye but sometimes wider; wider dorsally than ventrally. 43. Pronotum with dorsal preapical ridge rounded. 44. Mesepisternum with anterior surface sometimes reduced, slightly convex. 45. Pre-episternal groove curved, reaching scrobal level, not extending below. 46. Pterostigma somewhat longer and somewhat wider than prestigma; margin basal to vein r subparallel to costa; that within marginal cell straight (or slightly convex). 47. Marginal cell obliquely and rather broadly truncate at apex, much longer than distance from its apex to wing tip. 49. Submarginal cell 1 shorter (at least

slightly) than cell 2+3. 51. First recurrent vein far from first transverse cubital. 52. Forewing with cu-v two or three times longer than second abscissa M+Cu. 53. Hind wing with cu-v 1/4 to 1/5 as long as M+Cu. 54. Dorsal surface of propodeum about as long as metanotum. 55. Propodeal triangle very smooth, depressed medially. 57. Basitarsus 1 five to seven times longer than broad in male, about four times longer than broad in female; tarsomeres 2-4 unmodified. 59. Middle tibial spur of female about as long as basitarsus 2 or somewhat shorter, with coarse teeth (Fig. 10G); in male rather longer than half basitarsus length and with fine, dense teeth. 60. Basitarsus 2 of male longer than 1 or 3 (2 and 3 somewhat variable in female); tarsomeres 2-4 unmodified. 61. Tibia 3 of female somewhat less than twice as long as basitarsus 3, with keitrichia on inner surface except toward ventral and dorsal margins (Fig. 10F); male tibia 3 with keitrichia as in female. 62. Tibial scopa rather sparse, though dense on dorsal margin; outer surface with branched and simple hairs. 63. Hind tibial spurs (both sexes) with fine and dense teeth (appearing untoothed), slightly curved toward apices, outer somewhat shorter than inner. 64. Basitibial plate of male well defined. 65. Tarsus 3 with no modifications except basitarsus of female with apical process. 66. Claws bifurcate; rami subequal in male, inner much shorter than outer in female. 67. Metasoma in male somewhat wider than thorax. 69. T2-5 of male with gradulus posterolaterally not surpassing anterior half of tergum, not carinate, with postgradular depression on T2 and T3 well marked and narrow,

shallower on posterior terga; posterior marginal areas of T1-5 in male and T1-4 in female pilose, forming hair bands (sometimes weak in male); lateral fovea of T2 (both sexes) oval, weak (borders difficult to see). 70. Pygidial plate of male absent, represented only by an apically acute, smooth and bare area. 71. T7 of female squared (Fig. 10C). 72. T8 of male as in Figure 9H. 73. Metasomal sterna of male with hairs directed caudad, mostly on premarginal areas and not appressed, sparse or absent on midline. 73a. S1-5 of female with hairs short, dense and appressed, mixed with hairs somewhat longer, sparser, and not appressed (Fig. 10E). 74, 75. S4 and 5 of male with distal margins almost straight medially. 77. S6 of male with small apical emargination (Fig. 9E). 78. S6 of female with basal sclerotization long and very acute, duplication fully and strongly sclerotized, distal margin concave medially, S6 with patch of dense hairs on premarginal area, interrupted medially (Fig. 10H). 79. S7 of male with distal median projections short, proximal arms widely open (Fig. 9C). 80. S8 of male with median distal projection long, clavate, abruptly separated from a transversely rectangular body (Fig. 9D). 83. Gonocoxites globose, ventrally completely fused to each other. 84. Gonostylus fused to gonocoxite, short (almost 1/3 length of gonocoxite in ventral view). 85. Volsellae well developed, fused to each other forming a highly sclerotized plate, without denticles. 86. Penis valves with folds, somewhat intricate, rather rounded at apices; dorsally fused to each other by small and narrow bridge; laterally with a long row of hairs (Fig. 9A, B). 87. Penis usually reaching apex of penis valve or nearly so, narrower than valve, largely sclerotized, clearly separated from penis valve. 88. Sting elongate, truncate at apex, surpassing stylus (Fig. 10A, B).

*Comments.* Cockerell indicated that the type species of this genus is *Camptopoeum trifasciatum* Spinola, 1851 (now in *Liopoeum*). His description, however, corresponds to *Camptopoeum submetallicum* Spinola, 1851. Because of this misidentification the latter species has been considered for many years as the type species of *Acamptopoeum*. According to the International Code of Zoological Nomenclature, Article 70c, cases of misidentified type species have to be referred to the International Commission on Zoological Nomenclature for resolution. I will therefore request the International Commission to designate *Camptopoeum submetallicum* Spinola (= *C. trifasciatum* of Cockerell, not Spinola, 1851) as the type species of *Acamptopoeum*.

If the request is denied, then the name used by Cockerell in designating the type species must be

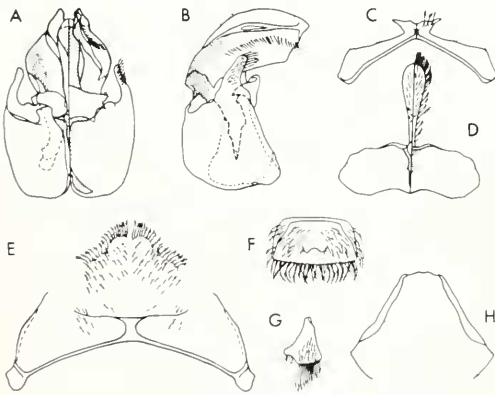


Figure 9. *Acamptopoeum submetallicum* (Spinola). Male: A, B, Genitalia, dorsal, ventral and lateral views; C, D, S7 and 8, dorsal and ventral views; E, S6, ventral view; F, Labrum; G, Labrum, lateral view; H, T8.

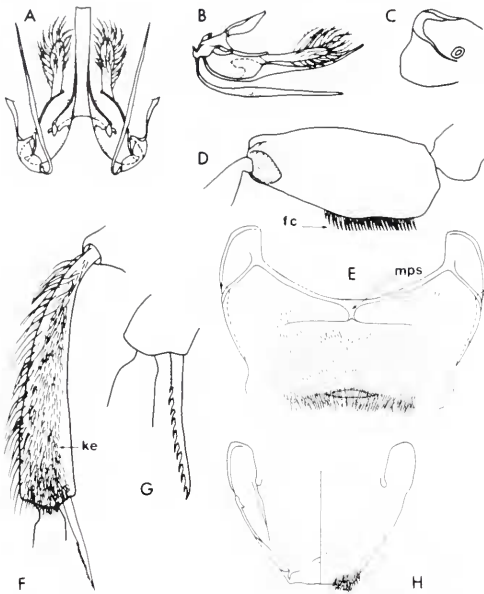


Figure 10. *Acamptopoeum submetallicum* (Spinola). *Female*: A, B, Sting, ventral and lateral views; C, T7; D, Femur 2 (hairs on inner surface omitted); E, S5, ventral view; F, Tibia 3, inner view; G, Spur, leg 2; H, S6, dorsal and ventral views. fc = femoral comb; ke = keirotrichia; mps = median proximal sclerotization.

maintained. In that case *Acamptopoeum* would contain the species here placed in *Calliopsis* (*Liopoeum*); *Liopoeum* would be a junior synonym. *Parafriesea* would stand as the generic name for the species now placed in *Acamptopoeum*.

The South American genus *Acamptopoeum* is represented by the following species: \**A. argentinum* (Friese, 1906a), \**A. prinii* (Holmberg, 1884), *A. inauratum* (Cockerell, 1926), *A. colombiensis* Shinn, 1965, *A. nigritarse* (Vachal, 1909), *A. vagans* (Cockerell, 1926), *A. maculatum* (Smith, 1853) (see Shinn, 1965), and \**A. submetallicum* (Spinola, 1851).

The type locality (east Florida) given for *A. maculatum* is not within the otherwise known range of the genus. It seems very unlikely that Florida is its real habitat (Shinn, 1967; Mitchell, 1960, under *Calliopsis*).

*Discussion.* *Acamptopoeum* is a distinctive genus although in the past its position has been confused. At first its species were considered as *Camptopoeum*, together with European and other South American species (Spinola, 1851); later it was treated as synonym of *Liopoeum* (Michener, 1944; Rozen, 1951, 1958).

Shinn (1967) noted that according to Moure (1956, personal communication to Shinn) *Acamptopoeum* constitutes "a clearcut group of closely related species." On the other hand, Shinn (1967) agrees with Michener (1944: 246) in considering the possibility that "*Parafriesea* = *Acamptopoeum* . . . is probably a mere subgenus of *Calliopsis*."

My study, however, does not support the idea of including *Acamptopoeum* in any other genus. The cladistic analysis indicates it to be the sister group of *Calliopsis* s. l. The cladogram (Fig. 30) shows that *Acamptopoeum*, in spite of the superficial similarity to some subgenera of *Calliopsis*, presents a series of apomorphies which support it as a good genus (see discussion in Cladistic Analysis section).

*Distribution.* This genus occurs in Argentina, Perú, Paraguay, Uruguay, Brazil, Colombia, and Chile (Moure, in litt.; Schrottky, 1903, 1913; Friese, 1906a, b; Holmberg, 1844, Shinn, 1965).

#### Genus *Calliopsis* Smith

*Diagnosis.* Superficially similar to *Acamptopoeum* but differing as follows: Pubescence of thorax usually shorter and less dense than in *Colletes*. Labrum usually with transverse ridge but not strongly salient. *Male*. S4 with distal margin produced medially (sometimes inconspicuously). S5 usually with well-developed median projection distally. *Female*. Sting not reaching stylus, tapered at apex.

*Description.* 3. Head, thorax, and legs usually with yellow marks. 8. Head broader than long (sometimes as broad as long in female). 20. Labrum with basal area glabrous. 33. Tentorial pit in outer subantennal suture, close to epistomal suture. 39. Orbits at least slightly convergent below, usually more strongly so in male; or in female sometimes subparallel. 41. Vertex at least slightly convex. 45. Pre-episternal groove not reaching scrobal level. 74. S4 of male with distal margin produced in the middle, sometimes inconspicuously so. 75. S5 of male with distal median projection, usually well developed (inconspicuous in *C. (Verbenapis)*). 80. S8 of male with two short, lateral projections between body and distal projection, sometimes very small. 84. Gonostylus absent.

*Discussion.* The genus *Calliopsis* is treated here in a new broad sense to include not only the subgenera *Calliopsis* s. str., *Perissander*, *Calliopsima* and *Verbenapis*, traditionally included in the genus, but also *Nomadopsis* s. str., *Macronomadopsis*, *Micronomadopsis*, *Hypomacrotera*, *Liopoeum* and two new subgenera *Liopoeodes* and *Ceroliopoeum*. This new concept of the genus *Calliopsis* is based on the following facts:

1. The similarity between some complex genitalic structures of *Nomadopsis* (in the former sense, as a genus) and those of some species of *Calliopsis* (in the usual sense) suggests that some species of *Nomadopsis* are more closely related to some *Calliopsis* than to other *Nomadopsis*. The cladogram (Fig. 30), however, still shows *Nomadopsis* (usual sense) as a monophyletic group, although the synapomorphies are not strong. Small ridges on the lateral part of the penis valve of males occur in *Micronomadopsis*, *Hypomacrotera*, *Calliopsis* s. str., *Perissander*, *Liopoeodes* and *Ceroliopoeum*. This fact may indicate a close relationship among these six taxa.

2. Chemosystematic studies indicate that, looking at the Dufour's gland lipids, the *Calliopsis*-*Nomadopsis*-*Hypomacrotera* group ("paraffin bees") appears to be monophyletic (Cane, 1983). The cladogram of this analysis shows one species of *Calliopsis* (usual sense) as being more closely related to one species of *Nomadopsis* than to two other species of *Calliopsis*.

3. Lack of strong characters to diagnose the traditional genera. *Calliopsis* and *Nomadopsis* (in the

old sense) have been characterized mainly by the presence of hair bands and of yellow integumental marks on the metasomal terga respectively. Both characters appear independently in other Panurginae. Larval characters also do not differentiate these groups (Rozen, 1966).

4. Existence of *C. (Liopoeodes) xenopous* n. sp., a species that does not fit within taxa already established. Maintaining generic rank for *Calliopsis*, *Nomadopsis* and *Hypomacrotera* leads to proliferation of genera difficult to separate from one another.

5. There is little morphological differentiation among the subgenera except for *Liopoeodes* and *Verbenapis*, which appear in the cladogram as having more apomorphies than the rest of the subgenera. There is no constant apomorphy for *C. (Micronomadopsis)*, which therefore may be paraphyletic.

6. The cladistic analysis indicates that *Calliopsis* s. l. is a natural group. The cladogram shows six synapomorphies (62, 81, 84, 85, 111, 115) that make this group monophyletic. The strongest characters are: 62, 81, 84, and 115.

KEY TO THE SUBGENERA OF THE GENUS *Calliopsis*

1. Males . . . . .	2
—Females . . . . .	12
2. Pubescence of basitarsus 3 on dorsal margin (at least in part) about as long as basitarsus or longer (Fig. 16A). Apical area of labrum clearly convex, almost glabrous except margin; labrum with no defined ridge separating basal and apical areas (Fig. 15H) . . . . .	<i>Liopoeum</i>
—Pubescence of basitarsus 3 on dorsal margin about half as long as basitarsus or shorter. Apical area of labrum hairy, rather flattened; labrum with ridge or carina separating basal and apical areas (Fig. 1F) [except entire labrum flat and pilose in <i>C. (H.) subalpina</i> ] . . . . .	3
3. T2-5 at least laterally with premarginal hair bands . . . . .	4
—T2-5 without premarginal hair bands . . . . .	7
4. Subantennal area black. Metanotum laterally without velvet area. Propodeal triangle basally smooth, concave medially . . . . .	<i>Verbenapis</i>
—Subantennal area yellow. Metanotum laterally with area (sometimes reduced to a small and narrow strip) of dense velvety hairs. Propodeal triangle basally rugose or at least slightly roughened. . . . .	5
5. Clypeus (lateral view) clearly protuberant (Figs. 1E, 8B). Metanotum laterally with conspicuous patch of velvet-brown hairs . . . . .	<i>Calliopsis</i> s. str.
—Clypeus (lateral view) almost flat. Metanotum laterally with small patch of velvet-white hairs . . . . .	6
6. Labrum with basal area delimited by strong carinate ridge. Basitarsus 2 somewhat shorter than 3. Propodeal triangle basally with strong striae; striated basal part delimited by strong transverse ridge . . . . .	<i>Calliopsima</i>
—Labrum with basal area delimited by weak ridge. Basitarsus 2 much longer than 3. Propodeal triangle basally with weak striae, posteriorly not delimited by strong transverse ridge . . . . .	<i>Perissander</i>
7. Metasoma without yellow marks. . . . .	8
—Metasomal terga usually with interrupted or complete yellow bands . . . . .	10
8. Antennal scape robust (Fig. 24F). Pterostigma (maximum width between costa and Rs) more than twice as broad as prestigma, side within marginal cell clearly convex (Fig. 2D) . . . . .	<i>Ceroliopoeum</i>

- Antennal scape normal. Pterostigma less than twice as broad as prestigma, side within marginal cell straight or nearly so (Fig. 2E) . . . . . 9
9. Inner orbits subparallel. Marginal cell about twice as long as submarginal cell 2+3 or longer. Tarsus 3 with tarsomeres 2-5 unmodified . . . . . *Hypomacrotera*
- Inner orbits convergent below (Fig. 22H). Marginal cell less than twice as long as submarginal cell 2+3. Tarsus 3 with basitarsus and tarsomeres 2-4 asymmetrical; distitarsus widened medially (Fig. 22K) . . . . . *Liopoeodes*
10. Tarsi 1, 2 with tarsomeres slender. Tarsus 3 often with tarsomeres 2-4 broadened laterally, asymmetrical (Fig. 21I) . . . . . *Micronomadopsis*
- Tarsi 1-3 with tarsomeres broadened distally, symmetrical . . . . . 11
11. Tibia 3 about twice as long as basitarsus 3. S4 clearly produced in middle of distal margin. S5 with well-developed median projection on distal margin (Fig. 18E) . . . . . *Nomadopsis*
- Tibia 3 somewhat longer than basitarsus 3. S4 inconspicuously produced in middle of distal margin. S5 distally with short median projection (Fig. 20H) . . . . . *Macronomadopsis*
12. Pterostigma (maximum width between costa and Rs) more than twice as broad as prestigma, margin within marginal cell clearly convex. Middle femur with ventral comb less than half length of femur. . . . . *Ceroliopoeum*
- Pterostigma less than twice as broad as prestigma, margin within marginal cell straight or nearly so. Middle femur with ventral comb about half length of femur . . . . . 13
13. T2-4 with premarginal hair bands at least laterally . . . . . 14
- T2-4 without premarginal hair bands . . . . . 19
14. Integument black (with some slight blue but no yellow). Wing venation mostly dark. Inner orbits subparallel (Fig. 23B). T1-2 polished, scarcely punctate . . . . . *Liopoeodes*
- Integument with at least some yellow marks. Wing venation mostly yellowish. Orbits convergent below. Terga with rather abundant punctation. . . . . 15
15. Middle tibial spur with coarse teeth distally (Fig. 16F). Tibia 3 with keitrichia on inner surface at base and at apex only (Fig. 16D). S6 distally with oblique patch of hairs beside midline (Fig. 16G) . . . . . *Liopoeum* (part)
- Middle tibial spur with teeth somewhat coarse distally (Fig. 14K). Tibia 3 with keitrichia on most of inner surface or absent toward ventral border. S6 distally with hairs forming a curved fringe . . . . . 16
16. Tarsus 1 on inner surface with hairs sparse, mostly stiff, curved and not tapered at apices (Fig. 14H). Metanotum laterally without patch of white, velvety hairs . . . . . *Verbenapis*
- Tarsus 1 on inner surface with hairs dense, unmodified. Metanotum laterally with small (sometimes inconspicuous) patch of white, velvety hairs . . . . . 17
17. Clypeus (lateral view) protuberant 1/3 width of eye or more. Paraocular area with lowest part noticeably wider than at level of antennal sockets, usually swollen on lower inner corner . . . . . *Calliopsis* s. str.
- Clypeus (lateral view) protuberant about 1/4 to 1/9 width of eye. Paraocular area with lowest part almost as wide as at level of antennal sockets, slightly convex . . . . . 18
18. Propodeum mostly punctate, at base conspicuously rugose and triangle delimited by strong ridge or carina. Metanotum laterally with patch of white velvety hairs clearly visible *Calliopsima*
- Propodeum posteriorly with extensive impunctate area, at base usually little or not very strongly rugose, triangle delimited by rather rounded ridge. Metanotum laterally with inconspicuous (difficult to see) patch of white, velvety hairs . . . . . *Perissander*
19. Middle tibial spur with most teeth much longer than those of hind tibial spurs (Fig. 16F). S6 distally with oblique patch of hairs beside midline (Fig. 16G) . . . . . *Liopoeum* (part)
- Middle tibial spur with most teeth only slightly longer than those of hind tibial spurs, fine or somewhat coarse (Fig. 17I). S6 distally with hairs forming a curved fringe (Fig. 17H) . . . . . 20
20. Propodeal triangle polished. Metasoma with no yellow markings. . . . . *Hypomacrotera*
- Propodeal triangle at least slightly rugose basally. Metasoma usually with complete or interrupted yellow integumental bands . . . . . 21
21. Body length less than 10 mm. Middle tibial spur with 4 teeth on distal half (Fig. 21H) . . . . . *Micronomadopsis*
- Body length 10 mm or longer. Middle tibial spurs with more than four (coarse or fine) teeth on distal half (Figs. 19D, 20J) . . . . . *Macronomadopsis* and *Nomadopsis*



**Subgenus *Calliopsis* Smith s. str.**

(Figs. 1A, B, D-F; 6B, 8B, 11, 12, 30)

*Calliopsis* Smith, 1853: 128. Type species: *Calliopsis andreniformis* Smith, 1853 (by designation of Ashmead, 1899: 85).

**Diagnosis.** Glossa somewhat shorter than prementum. Metasomal terga black, with distal hair bands. Axilla and metanotum laterally with dense patches of velvety hairs. *Male.* Basitarsus 2 somewhat longer than 1 and 3.

**Description.** 1. Length 5-8 mm. 3. Lower half of face, some spots on thorax (pronotum dorsally, pronotal lobe, tegula) and legs yellow in male, yellow much reduced in female. 4. Metasoma black. 5. Pubescence short, especially short and appressed on metasoma, forming premarginal bands on terga. 7. Punctures fine, well marked, dense on thorax. 8. Head broader than long and broader than thorax. 11. Glossa somewhat shorter than prementum. 13. Segment 1 of labial palp longer than 2-4 together. 16. Maxillary blade longer than prepupal part of galea. 17. Galeal comb of 17-26 bristles. 20. Labrum slightly protuberant, about twice as broad as long; basal area depressed, its distal margin a rounded ridge; labral apex somewhat inflexed.

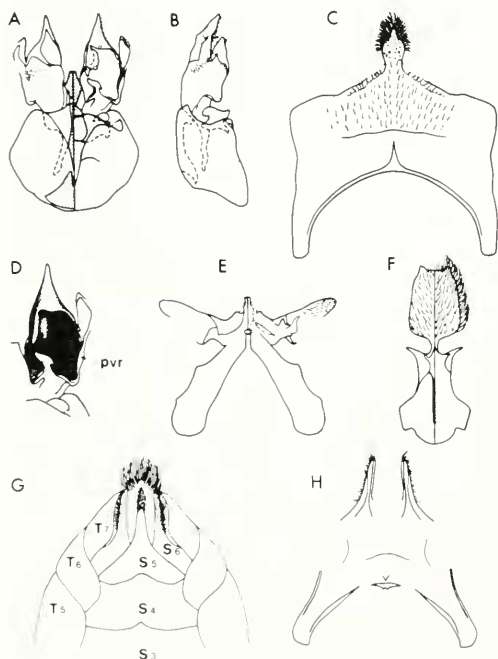


Figure 11. *Calliopsis (Calliopsis) andreniformis* Smith. *Male*: A, B, Genitalia, dorsal, ventral and lateral views; C, S5, ventral view; D, Penis valve; E, F, S7 and 8, dorsal and ventral views; G, Metasomal tip, ventral view; H, S6, ventral view. pvr = penis valve ridges.

27. Clypeus more than twice as broad as long, protuberant (about 1/3 width of eye in lateral view); distal margin with a rather small, pointed projection near lateral margin of labrum in male, rounded and bigger in female. 30. Inner subantennal suture curved. 31. Subantennal area wider than inner suture length and than antennal socket. 34. Antennal socket below middle of face. 36. Antennal flagellum of male unmodified (Fig. 12G); length variable (shorter than head as in *C. andreniformis* or longer); flagellomere 1 longer than 2 (almost twice as long or less) and about as long as broad. 37. Lower mesal paraocular area slightly convex to strongly swollen. 38. Facial fovea clearly visible, very narrow (almost linear). 40. Ocelli just above dorsal orbital tangent. 42. Gena of male (lateral view) narrower than eye, broader dorsally than ventrally. 43. Pronotum dorsally with preapical ridge rounded, developed only laterally, not strong. 43a. Axilla of male (lateral to scutellum) with patch of velvety, brown hairs. 43b. Metanotum laterally with velvety hairs forming a conspicuous brown patch in males, and small white patch in females. 44. Mesepisternum with anterior flat area reduced. 45. Pre-episternal groove deep, narrow, punctate. 46. Pterostigma somewhat longer than and about as wide as prestigma; side basal to vein r subparallel to costa, that within marginal cell straight. 47. Marginal cell narrowly truncate at apex, little longer than distance from its apex to wing tip. 49. Submarginal cell 1 about as long as cell 2+3 (or inconspicuously longer). 51. First recurrent vein not meeting first transverse cubital but sometimes very close to it. 52. Forewing with cu-v about three times longer than second abscissa M+Cu. 53. Hind wing with cu-v 1/4 to 1/5 as long as second abscissa M+Cu. 54. Dorsal surface of propodeum shorter than metanotum. 55. Propodeal triangle striate basally, not delimited by ridge or carina posteriorly. 57. Basitarsus 1 about seven to eight times longer than broad in male and about four to five times in female; tarsomeres 2-4 unmodified. 59. Middle tibial spur with minute and fine teeth, almost straight and longer than half length of basitarsus in female, slightly curved at apex and about 1/3 as long in male. 60. Basitarsus 2 of male somewhat longer than 1 and 3; in female basitarsus 1 as long as 2 and 3, tarsomeres 2-4 unmodified. 61. Tibia 3 of female about twice as long as basitarsus 3, inner surface with keirotichia except along ventral half; male tibia 3 with keirotichia on most of inner surface. 62. Tibial scopa of medium-sized, sparse, and mostly simple hairs. 63. Hind tibial spurs toothed similarly to middle one, somewhat curved, outer shorter than inner. 64. Basitibial plate of male well defined. 65. Basitarsus 3 of female with moderate apical projection; tarsomeres 2-4 unmodified. 66. Claws deeply cleft with rami subequal in male, inner ramus much shorter than outer in female. 67. Metasoma in male wider than thorax. 69. T2-5 of male with

gradulus posterolaterally reaching to middle of postgradular area at most, not strongly carinate and with postgradular depression rather shallow, narrow; posterior marginal areas of T1-5 in male and T1-4 in female each with hair band; lateral fovea of T2 (both sexes) slightly or well depressed, small and narrow in male, larger and wider in female. 70. Pygidial plate of male present. 71. T7 of female rather square, with no large dorsal, proximal expansion (Fig. 12B). 72. T8 of male similar to that of *Calliopsis*. 73. S1-5 of male with hairs mostly directed posteriorly; S6 pilose only on distal projections, mostly directed outward. 73a. S1-5 of female with hairs short, simple, appressed proximally; longer, branched, not appressed on pre-marginal and marginal areas medially. 75. S5 of male with a long and acute median apical projection, densely pilose at apex (Fig. 11C). 77. S6 of male distally with deep median emargination between two tapered projections (Fig. 11H). 78. S6 of female with basal sclerotization almost completely free from sternum; duplication thin, attached to a distal hardened area of sternum; distal margin produced in middle; S6 with distal hairs forming dense, somewhat curved band (Fig. 12C). 79. S7 of male with two distal (almost transverse), elongate projections (complex at base); proximal arms forming a V (Fig. 11E). 80. S8 of male with distal projection almost rectangular, with two small laterodistal lobes; body robust with two lateral curved and acute projections distally and with a weak median longitudinal ridge dorsally (Fig. 11F). 83. Gonocoxites globose, distally (ventral view) connected to one another by weakly sclerotized cuticle. 85. Volsellae attached to one another by slightly sclerotized cuticle, with no denticles. 86. Penis valves complex (with projections, folds, etc.), tapered distally, with minute ridges laterally (ven-

tral view) (Fig. 11A, D), fused dorsally by a narrow bridge. 87. Penis much shorter and narrower than valve, clearly separated from penis valve, somewhat sclerotized. 88. Sting not reaching stylus apex (Fig. 12D).

*Comments.* *Calliopsis* s. str. contains 12 described species (Shinn, 1967). The species that I studied in detail were: *C. (C.) andreniformis* Smith and *C. (C.) hondurasica* Cockerell.

*Discussion.* Shinn (1967) indicated that *Calliopsis* s. str. is most closely related to *Perissander*. This has been confirmed by the cladistic analyses presented here.

*Distribution.* This subgenus occurs from Panamá to Canada, and from the eastern United States to Utah, Nevada, California, and Baja California Sur.

### Subgenus *Perissander* Michener (Figs. similar to 11, 12; 30)

*Perissander* Michener, 1942: 275. Type species: *Calliopsis anomoptera* Michener, 1942 (monobasic and original designation).

*Diagnosis.* Similar to *Calliopsis* s. str. but differing as follows: Glossa much shorter than prementum. Only metanotum with narrow patch of dense hairs laterally. Propodeal triangle delimited by rounded ridge posteriorly. *Male.* Forewing sometimes brown at apex. Basitarsus 2 much longer than 1 or 3.

*Description.* As in *Calliopsis* s. str. except: 3. Wing tip of male sometimes brown as in male of *Hypomacrotera*. 4. Metasoma sometimes fully or partially reddish. 7. Punctures of metasoma of male somewhat denser than those of *Calliopsis* s. str. 11. Glossa much shorter than prementum. 13. Segment 1 of labial palp about as long as 2-4 together. 16. Maxillary blade tapered abruptly at apex, slightly shorter than prepupal part of galea. 17. Galeal comb of 11 bristles. 20. Labrum of male sometimes almost flat [e.g., in *C. (P.) anomoptera*] with basal area narrow and with distal margin a weak ridge. 27. Clypeus about three times broader than long, little protuberant (about 1/5 or 1/6 width of eye in lateral view); distal margin with a rounded projection near lateral margin of labrum, little developed in male. 30. Inner subantennal suture angulate. 31. Subantennal area about as wide as antennal socket. 36. Antennal flagellum of male as long as or slightly shorter than head; flagellomere 1 about as long as 2. 37. Lower mesal paraocular area somewhat convex. 38. Facial fovea of variable shape. 43b. Metanotum with narrow patch of dense hairs laterally (usually hidden by base of hind wing). 45. Pre-episternal groove shallow. 46. Pterostigma about as long as prestigma. 47. Marginal cell about as long as to much longer than distance from its apex to wing tip. 51. First recurrent vein not as close to first transverse cubital as in *C.*

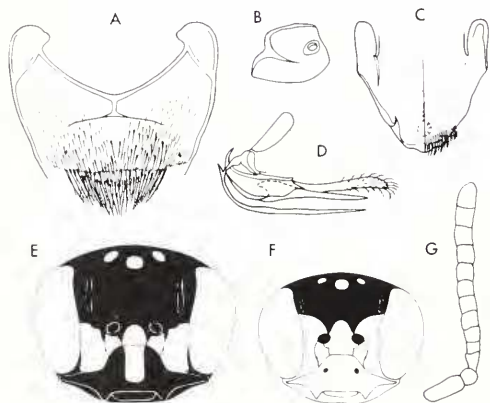


Figure 12. *Calliopsis (Calliopsis) andreniformis* Smith. *Female:* A, S5, ventral view; B, T7; C, S6, dorsal and ventral views; D, Sting; E, Head, frontal view. *Male:* F, Head, frontal view; G, Antenna.

*andreniformis* Smith. 52. Forewing with cu-v about half to twice as long as M+Cu. 54. Dorsal surface of propodeum longer than metanotum. 55. Propodeal triangle basally with weak striae, in middle delimited by ridge posteriorly. 59. Middle tibial spur with few and sparse teeth in female and about 1/5 as long as basitarsus 2 in male. 60. Basitarsus 2 of male much longer than 1 and 3. 61. Tibia 3 of female less than twice as long as basitarsus 3. 63. Hind tibial spurs generally with fine teeth (sometimes somewhat coarse). 66. Claws in male with rami short, subequal on legs 1 and 3, inner shorter than outer on leg 2. 75. S5 of male with distal, median projection sometimes somewhat rounded at apex. 78. S6 of female with distal margin concave in the middle. 80. S8 of male with only one small median lobe at apex. 85. Volsellae fully fused to each other distally, connected proximally by weakly sclerotized cuticle.

*Comments.* There are seven described species in this subgenus (Shinn, 1967). I studied in detail: *C. (P.) anomoptera* Michener, *C. (P.) gilva* Shinn and *C. (P.) rogeri* Shinn.

*Discussion.* The subgenus *Perissander*, as noted above and in Figure 30, is closely related to *Calliopsis* s. str. and both together are the sister group of the subgenera *Liopoeum*, *Hypomacrotera*, *Micronomadopsis*, *Macronomadopsis*, *Nomadopsis* s. str., *Ceroliopoeum*, and *Liopoeodes*. The metanotal velvet area of males, so well developed in *Calliopsis* s. str., is small, less dense, and rather difficult to see, although still present, at least in the species that I studied. This is in disagreement with Shinn (1967) who has stated that this pilose area is absent in this subgenus.

*Distribution.* *Perissander* is found in the southwestern United States and northwestern México, including Baja California (Shinn, 1967).

### Subgenus *Calliopsima* Shinn (Figs. 13, 30)

*Calliopsima* Shinn, 1967: 834. Type species: *Calliopsis rozeni* Shinn, 1967 (original designation).

*Diagnosis.* Differs from *Calliopsis* s. str. as follows: Glossa longer than prementum. Clypeus flattened. Labrum with distal margin of basal area a strong carina. Metanotum basilaterally with narrow patch of dense hairs. Basitarsus 2 shorter than 3. *Male.* Labral apex short.

*Description.* Agrees with description of *Calliopsis* s. str. except: 1. Length 7-8 mm. 5. Pubescence denser on metasoma. 7. Punctures dense on metasoma of both sexes. 11. Glossa longer than prementum. 13. Segment 1 of labial palp about twice as long as 2-4 together. 16. Maxillary blade longer than prepalpal part of galea. 17. Galeal comb of 13 bristles. 20. Labrum of male with basal area large and slightly depressed; distal margin of basal area (both sexes) usually a strong

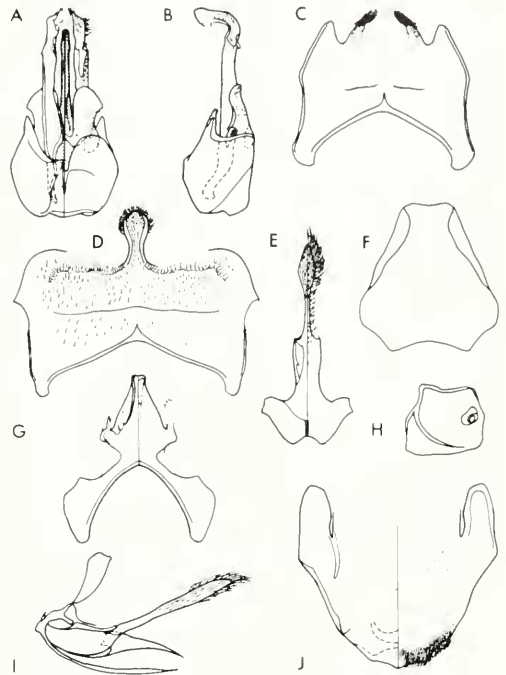


Figure 13. *Calliopsis (Calliopsima) rozeni* Shinn. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, D, S6 and S5, ventral views; E, F, S8, dorsal and ventral views; G, H, S7, dorsal and ventral views. *Female:* I, Sting; J, S6, dorsal and ventral views.

carina; apex of labrum very narrow in male, wider in female. 27. Clypeus flattened (about 1/9 width of eye in lateral view); distal margin with projection near lateral margin of labrum rounded, similar to that of *Perissander*. 31. Subantennal area about twice as wide as inner suture length and slightly wider than antennal socket. 36. Antennal flagellum of male somewhat shorter than head; flagellomere 1 somewhat longer than 2 and slightly wider than long. 37. Lower mesal paraocular area rather flat or slightly convex. 45. Pre-episternal groove rather wide and shallow. 46. Pterostigma less than twice as broad as prestigma. 47. Marginal cell longer than in *Calliopsis* s. str. 49. Submarginal cell 1 somewhat longer to shorter than cell 2+3. 51. First recurrent vein clearly distant from first transverse cubital. 52. Forewing with cu-v longer than second abscissa M+Cu. 54. Dorsal surface of propodeum longer than metanotum. 55. Propodeal triangle striate laterally, rugose medially, posteriorly delimited by carina. 57. Basitarsus 1 about six to seven times longer than broad in male and about four times in female. 59. Middle tibial spur about half as long as basitarsus 2. 60. Basitarsus 2 in both sexes longer than 1 and shorter than 3. 61. Tibia 3 of female less than

twice as long as basitarsus. 62. Tibial scopa of medium-sized, dense, branched hairs. 69. T2-5 of male with gradulus long and distinctly carinate; postgradular depression rather deep on T2-3; fovea of T2 clearly visible, in female only slightly bigger and not much wider than that of male. 71. T7 of female rather squared (Fig. 13H). 75. S5 of male with median apical projection, rather short and clavate (Fig. 13D). 77. S6 of male with distal margin broadly produced medially; with two short distal mesal lobes (Fig. 13C). 79. S7 of male with distal area triangular, laterally with a weakly sclerotized elongate projection; proximal arms forming a V (Fig. 13G). 80. S8 of male with distal projection long and narrow except arrowhead-shaped at apex; body of S8 with latero-distal projections acute but very small (Fig. 13E). 85. Volsellae strongly developed (of different shape and much larger than in *Calliopsis* s. str. and *Perissander*), fused to each other proximally, free distally, with no denticles. 86. Penis valves long, rather simple, angulate at apex, attached to each other dorsally by reduced membranous area. 87. Penis long, narrower than valve. 88. Sting even shorter than in *Calliopsis* s. str. (much shorter than stylus) (Fig. 13I).

**Comments.** The subgenus *Calliopsisima* contains 15 species (Shinn, 1967). *C. (C.) rozeni* Shinn and *C. (C.) coloradensis* Cresson were examined in detail.

**Discussion.** The cladogram (Fig. 30) shows that the subgenus *Calliopsisima* is the sister group of the other subgenera of *Calliopsis* s. l. (based on male characters only) but is more closely related to *Verbenapis* than to *Calliopsis* s. str. and *Perissander* together. The relationships among these subgenera agree with those stated by Shinn (1967).

**Distribution.** According to Shinn (1967) *Calliopsisima* occurs from Canada to southern México.

### Subgenus *Verbenapis* Cockerell and Atkins (Figs. 14, 30)

*Verbenapis* Cockerell and Atkins, 1902: 44. Type species: *Calliopsis verbenae* Cockerell and Porter, 1899 (monobasic).

**Diagnosis.** Genital and associated sterna more similar to those of *Calliopsisima* than to those of *Calliopsis* and *Perissander*. It differs from these subgenera as follows: Metanotum laterally without velvety hairs. Subantennal and supraclypeal areas black. Glossa as in *Calliopsisima*. **Male.** Basitarsus 2 shorter than 3 (as in *Calliopsisima*). S6 with median projection with minute median distal emargination. **Female.** Tarsus 1 on inner surface with rigid hairs, curved at blunt apices.

**Description.** Agrees with that of *Calliopsis* s. str. except: 1. Length 7-8 mm. 3. Face with yellow marks restricted to clypeus and lower paraocular area; thorax black; legs with yellow reduced,

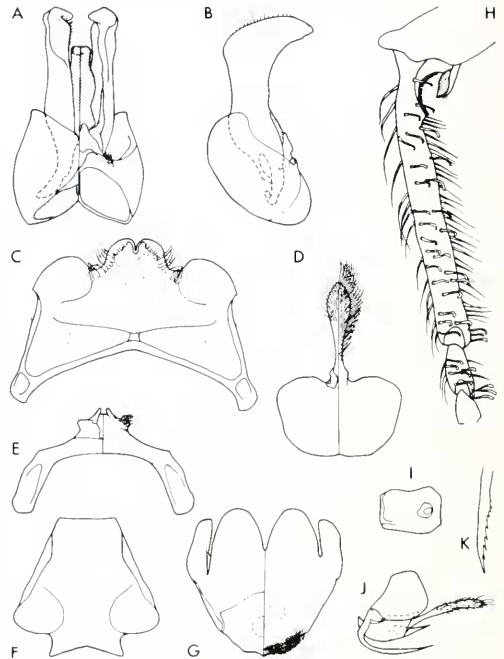


Figure 14. *Calliopsis (Verbenapis) verbenae* Cockerell and Porter. **Male:** A, B, Genitalia, dorsal, ventral and lateral views; C, S6, ventral view; D, E, S8 and 7, dorsal and ventral views; F, G, T8. **Female:** H, Tarsus 1, inner view; I, T7; J, Sting; K, Spur, leg 2.

although extensive in male. 5. Tergal hair bands less dense in male. 7. Punctures sparser on thorax and metasoma. 11. Glossa longer than prementum as in *Calliopsisima*. 13. Segment 1 of labial palp more than three times longer than 2-4 together. 16. Maxillary blade more than twice as long as prepupal part of galea. 17. Galeal comb of 18 bristles. 20. Labrum of male similar to that of *Calliopsisima*; in female, basal area well depressed and with weaker distal ridge. 27. Clypeus somewhat protuberant (about 1/4 width of eye in lateral view); distal margin with a small rounded projection near lateral margin of labrum as in *Perissander*. 36. Antennal flagellum of male similar to that of *Calliopsisima*. 37. Lower mesal paraocular area somewhat convex as in *Perissander*. 38, 45, 46, 47. Facial fovea, pre-episternal groove, pterostigma, and marginal cell as in *Calliopsisima*. 49. Submarginal cell 1 somewhat longer than cell 2+3. 51. First recurrent vein somewhat distant from first transverse cubital. 52. Forewing with cu-v longer (about twice) than second abscissa M+Cu. 55. Propodeal triangle polished, shiny, with deep median concavity. 57. Basitarsus 1 about eight times longer than broad in male and about seven times in female, inner surface with

curved hairs in female; tarsomeres of female (inner surface) with hairs as on basitarsus. 58. Femur of female with comb of hairs shorter than in *Calliopsis* s. str. 59. Middle tibial spur with teeth serrate (Fig. 14K), sparser than in *Calliopsis* s. str., similar to that of *Perissander*. 60. Basitarsus 2 of male as in *Calliopsima*; female with basitarsus 2 as long as 1 and 3. 61, 62. Tibia 3 of female and tibial scopa similar to those of *Calliopsima* but scopa of sparser hairs with shorter branches. 67. Metasoma in male similar to that of *Calliopsis* s. str. but only slightly wider than thorax. 69. T2-5 of male with gradulus short; that of T2 (both sexes) indistinct, difficult to see. 70. Pygidial plate of male present. 71. T7 of female as in Figure 14I. 72. T8 of male as in Figure 14F. 74. S4 of male with distal margin inconspicuously produced in middle (difficult to see). 75. S5 of male with distal margin little produced medially, with no projection as in the other subgenera of *Calliopsis*. 77. S6 of male with a small median emargination (Fig. 14C). 78. S6 of female similar to *Calliopsis* but duplication somewhat sclerotized (Fig. 14G). 79. S7 of male similar to that of *Calliopsima* but distal area shorter and with no lateral elongated projection (Fig. 14E). 80. S8 of male with distal projection elongate, clavate; proximal area almost rectangular with no projections but small bumps (Fig. 14D). 85. Volsellae almost fully fused, well sclerotized medially, with no denticles. 86. Penis valves similar to those of *Calliopsima* but wider (especially in lateral view), dorsally fused to each other through a narrow sclerotized bridge. 87. Penis long, but somewhat wider than in *Calliopsima*, narrower than valve. 88. Sting extremely short (Fig. 14J).

**Comments.** The subgenus *Verbenapis* comprises four species (Shinn, 1967; Hurd, 1979). *C. (V.) verbenae* Cockerell and Porter, *C. (V.) nebraskensis* Crawford and *C. (V.) micheneri* Shinn were available for this study.

**Discussion.** *Verbenapis* is, according to the cladogram (Fig. 30), the sister group of the remaining subgenera of *Calliopsis*. On one hand it is the most closely related to *Calliopsima*; on the other hand it is the closest relative of *Acamptopoeum*. This is in disagreement with Shinn (1967), who stated that *Calliopsima* has a mixture of the characters found in *Calliopsis* s. str. and *Acamptopoeum*.

*Verbenapis*, however, is the subgenus that possesses the most characters agreeing with those of *Acamptopoeum*. *Verbenapis* has the propodeal triangle smooth, concave medially, and lacks the metanotal pad of hairs, as in *Acamptopoeum*. At the same time other characters seem transitional in *Verbenapis*. For example, S6 in *Acamptopoeum* has a very small distal, median emargination; in *Verbenapis* the same area is slightly sclerotized, with two small, weakly differentiated lobes laterally (Fig. 14C), while in *Calliopsima* the lateral lobes of S6

are well developed and the apical margin clearly concave. Finally, in the subgenera *Calliopsis*, *Perissander*, *Liopoeum*, *Hypomacrotera*, *Micronomadopsis*, *Ceroliopoeum* and *Liopocodes*, S6 has elongate, acute lateral projections and a strongly concave margin medially. A similar gradual progression is shown by S8.

**Distribution.** United States (except southeast and west) and México (Shinn, 1967).

### Subgenus *Liopoeum* Friese (Figs. 15, 16, 30)

*Liopoeum* Friese, 1906b: 176. Type species: *Camptopoeum hirsutulum* Spinola, 1851 (by designation of Sandhouse, 1943: 564).

**Diagnosis.** Close to *Hypomacrotera* but differing as follows: Pubescence long, especially on legs. **Male.** Tarsus 3 with tarsomeres 2-4 expanded laterally. Terga with or without yellow marks. S5 with distal median projection long, truncate or tapered at apex. **Female.** Middle tibial spur with sparse and usually coarse teeth. Tibia 3 on inner

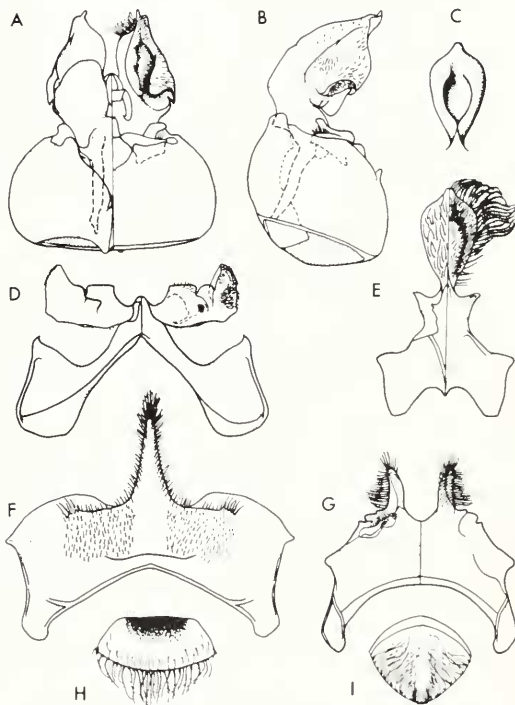


Figure 15. *Calliopsis (Liopoeum) hirsutulum* (Spinola). **Male:** A, B, Genitalia, dorsal, ventral and lateral views; C, S8, apex, ventral view (hairs omitted); D, E, S7 and 8, dorsal and ventral views; F, S5, ventral view; G, S6, dorsal and ventral views; H, Labrum; I, T7 apex.

surface with keirotichia dense at proximal and distal ends, sometimes present toward dorsal margin but sparse. S6 with distal patch of oblique hairs (in well-organized rows) at each side of produced median area.

*Description.* 1. Length 5–8 mm. 3. Lower half of face, pronotum (sometimes) and legs with yellow marks; spot on paraocular area (both sexes) extending up beside orbit as in *Acampoptoeum* (male); spots of female usually more reduced on face than in male, absent on thorax. 4. Metasoma with or without yellow marks on terga. 5. Pubescence usually long on head and thorax and especially so on legs; usually shorter on metasoma. 7. Punctures fine, usually much sparser on metasomal terga. 8. Head wider than thorax (about as wide as thorax in female of *C. (L.) trifasciata* (Spinola) and an undescribed Chilean species from Bio-Bio area). 11. Glossa longer than half length of prementum. 13. Segment 1 of labial palp usually slightly longer than 2–4 together. 14. Segment 2 of labial palp less than twice as long as 3. 16. As in *Calliopsis* s. str. 17. Galeal comb of 16–19 bristles. 20. Labrum similar to that of *Calliopsis* s. str. but with no well-defined ridge (Fig. 15H). 27. Clypeus more than twice as broad as long and somewhat to slightly protuberant (1/3 to 1/6 width of eye in lateral view); distal margin with an acute or rounded projection near lateral margin of labrum. 30. Inner subantennal suture angulate or strongly curved. 31. As in *Calliopsis* s. str. 34. Antennal socket about middle of face in female, below middle in male. 36. Antennal flagellum of male unmodified, longer than head; flagellomere 1 about as long as 2 and about as long as broad (slightly longer in an undescribed Chilean species). 37. Lower paraocular area similar to that of *Acampoptoeum*. 38. Facial fovea variable (oval with borders not well delimited or narrow and well defined in an undescribed Chilean species). 40. Ocelli above dorsal orbital tangent except tangent crossing the middle ocellus in undescribed Chilean species. 42. Gena of male (lateral view) about as broad as, or broader than eye, dorsally wider than ventrally. 43, 44. As in *Calliopsis* s. str. 45. Pre-episternal groove weak (sometimes seen only as a smooth strip). 46. Pterostigma longer than and slightly less than twice as broad as prestigma; otherwise as in *Calliopsis* s. str. 47. Marginal cell somewhat obliquely truncate at apex, much longer than distance from apex to wing tip. 49. Submarginal cell 1 longer than cell 2 + 3. 51. As in *Calliopsis* s. str. 52. Forewing with cu-v longer than second abscissa M + Cu. 53. Hind wing with cu-v about 1/3 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum about as long as metanotum. 55. Propodeal triangle basally smooth, microareolate, or with striae (sometimes depressed medially). 57. Basitarsus 1 five to six times longer than broad in male and about four times in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur of female

with sparse and usually coarse teeth (Fig. 16F) (not very coarse in undescribed Chilean species), about as long as basitarsus 2 or slightly shorter; in male with very fine and dense teeth, about 1/2 basitarsal length. 60. Basitarsus 2 of both sexes about as long as 1 and somewhat shorter than or as long as 3; tarsomeres 2–4 unmodified. 61. Tibia 3 of female less than twice as long as basitarsus 3, inner surface with keirotichia at proximal and distal ends (almost absent medially); male tibia 3 with keirotichia on most of inner surface. 62. Similar to that of *Calliopsis* s. str. 63. Hind tibial spurs (both sexes) with fine teeth (denser in male), almost straight or clearly curved toward apex, outer slightly shorter than inner. 64. Basitibial plate of male distinguishable, though margins not strongly developed (weaker in undescribed Chilean species). 65. Basitarsus 3 unmodified; tarsomeres 2–4 in male expanded laterally (at least slightly), in female unmodified. 66, 67. Similar to those of *Calliopsis* s. str. 69. T2–5 of male with gradulus posterolaterally short and weak (or almost absent) and postgradular depression narrow, rather shallow; posterior marginal areas of T1–5 in male and T1–4 in female usually scarcely pilose; terga of female sometimes with distal hair bands; lateral fovea of T2 (both sexes) narrow, slightly depressed. 70. Pygidial plate of male recognizable, short, not well delimited laterally, truncate or rounded at apex (Fig. 15I). 71. T7 of female as in Figure 16C. 72. T8 of male similar to that of *Hypomacrotera*. 73. S1–5 of male with hairs directed posteriorly, very short (except longer distally), present mostly on lateral areas; on S6 mostly directed obliquely outward, on distal projections only. 73a. S1–5 of female with hairs as in *Acampoptoeum*. 75. S5 of male, on distal margin, with long median projection; projection truncate or tapered and densely pilose apically (Fig. 15F). 77. Similar to that of *Calliopsis* s. str. 78. S6 of female as in *Calliopsis* s. str. but with distal hairs forming a dense oblique patch (several well-organized rows), absent on midline (Fig. 16G). 79. S7 of male with distal lateral projections intricate, with minute, dense hairs at apex and small brush of longer hairs medially; proximal arms forming a V (Fig. 15D). 80. S8 of male with distal projection with apical long hairs, deeply concave ventrally (Fig. 15C, E). 83. Gonocoxites globose, in ventral view fused to each other proximally, connected by membrane distally; in dorsal view, proximally with a well-developed mesal projection. 85. Volsellae well developed, fused to each other by a narrow firm bridge distally, by membrane proximally, with few denticles. 86. Penis valves complex (intricate, with folds), tapered toward apices; dorsally fused to each other by small and narrow bridge. 87. Similar to that of *Calliopsis* s. str. 88. Sting elongate, reaching but not surpassing apex of stylus (Fig. 16B).

*Comments.* The subgenus *Liopoeum* contains a few described species, most of which have been

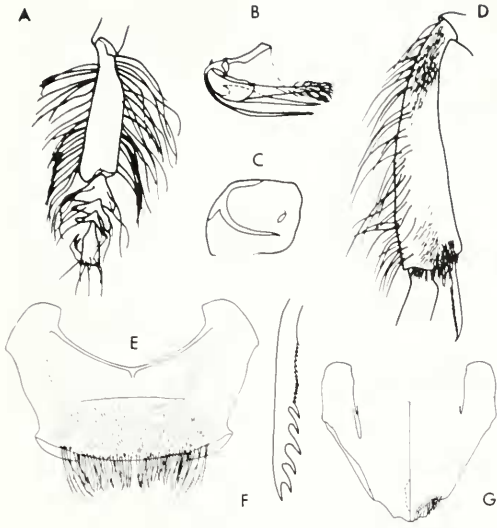


Figure 16. *Calliopsis (Liopoeum) hirsutululum* (Spinola). *Male*: A, Tarsus 3. *Female*: B, Sting; C, T7; D, Tibia 3, inner view; E, S5, ventral view; F, Spur, leg 2; G, S6, dorsal and ventral views.

placed erroneously in *Camptopoeum* (see Spinola, 1851). (*Camptopoeum* is palearctic and not in the Calliopsini.) Friese (1908) segregated *Liopoeum* as a subgenus of *Camptopoeum* for some South American species. However, they were still mixed with species of other genera.

The described species now recognized as belonging to the subgenus *Liopoeum* are: \**C. (Liopoeum) argentina* (Jørgensen), \**hirsutulula* (Spinola), \**mendocina* (Jørgensen), and \**trifasciata* (Spinola) (all new combinations).

**Discussion.** Among the subgenera of *Calliopsis*, *Liopoeum* is one of the most distinctive. Some species in this subgenus have hair bands on the metasomal terga of females, while others have tergal yellow marks, and no hair bands. This fact indicates that the presence or absence of these characters may not be useful or diagnostic at the subgeneric level.

**Distribution.** *C. (Liopoeum)* occurs in Argentina and Chile.

#### Subgenus *Hypomacrotera* Cockerell and Porter (Figs. 2E, 17, 30)

*Hypomacrotera* Cockerell and Porter, 1899: 418. Type species: *Hypomacrotera callops* Cockerell and Porter, 1899 (original designation).

**Diagnosis.** Metasoma without yellow marks [red in *C. (H.) subalpina* (Cockerell)]. Pilosity short. Marginal cell narrowly truncate and much longer than distance from its apex to wing tip.

Pterostigma with sides parallel. *Male*. Tarsus 3 unmodified. Forewing tip dark brown. S5 distally with median elongate tapered projection. *Female*. Middle tibial spur with fine and dense teeth. S6 distally with rounded fascia of dense hairs.

**Description.** Agrees with description of subgenus *Liopoeum* except: 1. Length 5–8 mm. 3. Lower part of face (approximately 1/3) yellow (or whitish); apex of forewing in male brown. 4. Metasoma without yellow marks [red in *C. (H.) subalpina*]. 5. Pubescence in general short; much shorter on metasoma than on rest of body. 7. Punctures rather dense on metasomal terga. 13. Segment 1 of labial palp somewhat longer than 2–4 together. 17. Galeal comb of 10–16 bristles. 20. Labrum less than twice as broad as long; male with basal area and ridge in *C. (H.) callops* (Cockerell and Porter), similar to that of *Liopoeum* but flat, in *C. (H.) subalpina* more extensively pilose; female with well-developed ridge. 27. Clypeus width more than three to five times broader than long, rather flattened (lateral view). 30. Inner subantennal suture angulate. 31. Subantennal area broader than inner suture length and about as wide as (or slightly wider than)

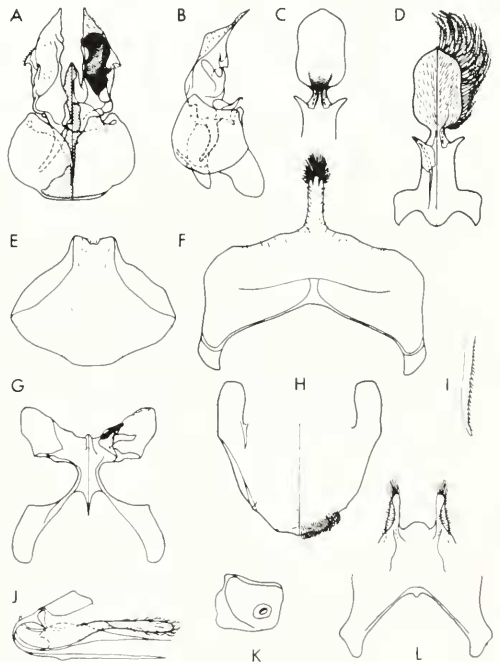


Figure 17. *Calliopsis (Hypomacrotera) callops* (Cockerell and Porter). *Male*: A, B, Genitalia, dorsal, ventral and lateral views; C, S8, tip (hairs omitted); D, S8, dorsal and ventral views; E, T8; F, S5, ventral view; G, S7, dorsal and ventral views; H, S6, dorsal and ventral views; I, Spur, leg 2; J, Sting; K, T, Tibia 3, dorsal and ventral views.

socket. 34. Antennal socket approximately at middle of face. 36. Flagellomere 1 slightly longer than broad (or about as wide as long). 37. Lower paracocular area similar to that of *Acamptopocum*. 38. Facial fovea oval, weakly differentiated. 39. Orbits convergent below, slightly so in *C. (H.) subalpina*. 40. Ocelli just above dorsal orbital tangent. 42. Gena of male (lateral view) nearly as wide as eye; somewhat wider dorsally than ventrally. 45. Pre-episternal groove weak, short, not reaching scrobal level. 46. Pterostigma longer than and about as wide as prestigma (or somewhat less than twice as broad as prestigma). 47. Marginal cell narrowly and transversely truncate at apex, longer than distance from its apex to first transverse cubital. 53. Hind wing with cu-v 1/4 to 1/5 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum similar to that of *Liopocum* but somewhat variable. 55. Propodeal triangle basally smooth, depressed medially, glabrous. 57. Basitarsus 1 three times longer than broad in female. 59. Middle tibial spur of female slightly more than half length of basitarsus 2, with fine and dense teeth (Fig 17I); of male toothed as in female but less than half basitarsal length. 60. Basitarsus 2 of male longer than 1 and somewhat shorter than 3; of female as in male but sometimes basitarsus 2 about as long as 3. 61. Tibia 3 of female on inner surface with keirotrichia except toward ventral margin. 62. Tibial scopa of sparse, rather short and apparently simple hairs on outer surface, inconspicuously branched and somewhat longer on margins. 63. Hind tibial spurs (both sexes) almost straight. 65. Tarsus 3 with no modifications. 69. Male with postgradular depression deep on T2, shallow on T3-5; posterior marginal areas of T1-5 in male and T1-4 in female pilose; terga (both sexes) with no hair bands; lateral fovea of T2 (both sexes) weakly depressed, somewhat wider in female. 70. Pygidial plate of male well developed in *C. (H.) subalpina*, in *C. (H.) callops* only distinguishable at apex. 71. T7 of female rather squared, with dorsal, proximal area not greatly expanded (Fig. 17K). 75. S5 of male with median elongate projection tapered (Fig. 17F). 78. S6 of female with distal hairs longer than in *Liopocum* and arranged in well-defined, curved band of dense hairs (Fig. 17H). 79. S7 of male with no patch of hairs forming a distal brush and with median small spine-like projection between proximal long arms (Fig. 17G) [absent in *C. (H.) subalpina*]. 80. S8 of male with distal part ventrally concave only at base, with hairs shorter than in *Liopocum* (Fig. 17C, D). 83. Gonocoxite dorsally, on proximal area, with no mesal projection in *C. (H.) callops* [but present in *C. (H.) subalpina*]. 86. Penis valves with ridges medially on outer margin (ventral view) (Fig. 17A).

**Comments.** Only two species of this subgenus are recognized: \**C. (H.) callops* (Cockerell and Porter) and \**C. (H.) subalpina* (Cockerell) (new

combinations), each with two subspecies (Hurd, 1979). Because of size and metasomal color, the two species are superficially very different. Nonetheless, they are closely related.

Until now *Hypomacrotera* has been poorly characterized, the major diagnostic character having been the infuscated area at the apex of the forewing in males. This character is not strong, since a brown spot on the apex of the forewing also appears in males of some species of *Calliopsis* s. str., *C. (Perissander)*, and in *C. (Liopocodes) xenopous*, n. sp. The latter species has characters that are a mixture of those of *Hypomacrotera*, *Liopocum*, and *Calliopsis* s. str.

The cladogram (Fig. 30) shows that the subgenus *Hypomacrotera* is more closely related to *Liopocum* than to other subgenera of *Calliopsis*. Rozen (1970) indicates that *Hypomacrotera* coats pollen masses with a waterproof substance as do other *Calliopsis*.

**Distribution.** *C. (Hypomacrotera)* occurs in the southwestern United States (Colorado, New Mexico, Arizona, California) and México (Baja California and Sonora) (Hurd, 1979).

### Subgenus *Nomadopsis* Ashmead

(Figs. 18, 19, 30)

*Nomadopsis* Ashmead, 1898: 285. Type species: "*Perdita*" *zonalis* Cresson, 1879 (monobasic and original designation), *lapsus* for *Calliopsis zonalis* Cresson, 1879.

*Spinoliella* subg. *Claremontiella* Cockerell, 1933: 25. Type species: *Spinoliella euxantha* Cockerell, 1933 = *Calliopsis zonalis* Cresson, 1879 (monobasic and original designation).

**Diagnosis.** Metasomal terga with yellow bands. Sterna with hairs mostly short, straight, appressed. Differs from *Macronomadopsis* as follows: **Male.** Tarsus 1 and 2 with tarsomeres 2-4 widened distally. Tarsus 3 similar to 1 and 2, symmetrical. S4 and S5 with distal produced area well developed.

**Description.** 1. Length 7-12 mm. 3. Lower part of face, some areas of thorax (pronotum, tegula), and legs with yellow marks, reduced in female. 4. Metasoma with complete or interrupted yellow bands. 5. Pubescence in general short; dense, mostly very short and appressed on sterna. 7. Punctures mostly fine, well marked, smaller and usually dense on metasoma. 8. Head nearly as broad as thorax, sometimes narrower in female. 11. Glossa longer than prementum (flabellum present in several species). 13. Segment 1 of labial palp more than two to five times longer than 2-4 together. 16. Maxillary blade more than twice as long as prepalpal part of galea. 17. Galeal comb of 18-23 bristles. 20. Labrum broader than long; basal area depressed; distal margin of basal area a rounded ridge; labral apex convex, inflexed. 27.



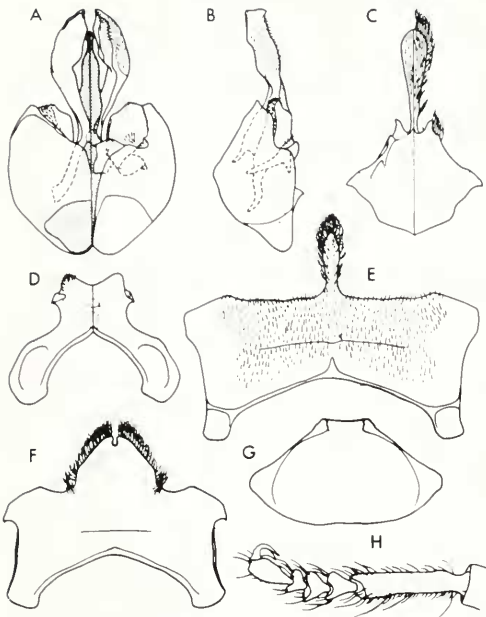


Figure 18. *Calliopsis (Nomadopsis) zonalis* Cresson. Male: A, B, Genitalia, dorsal, ventral and lateral views; C, D, S8 and 7, dorsal and ventral views; E, F, S5 and 6, ventral view; G, T8; H, Tarsus 3.

Clypeus more than twice as broad as long, protuberant (usually  $1/2$  width of eye in lateral view in male and usually  $1/3$  in female, except almost flat in both sexes of *C. (N.) edwardsii* Cresson; distal margin with a rounded projection beside lateral margin of labrum. 30. Inner subantennal suture curved or somewhat angulate. 31. Subantennal area about as wide as inner suture length and at least slightly wider than antennal socket. 34. Antennal socket somewhat below middle of face. 36. As in *Calliopsis* s. str. but flagellomere 1 longer than 2, about as long as broad or little longer. 37. Lower mesal paraocular area somewhat swollen to almost flat. 38. Facial fovea rather deep, narrow. 39. Orbits sometimes subparallel in female. 40. Ocelli fully or mostly above dorsal orbital tangent. 42. Gena of male (lateral view) little wider to little narrower than eye; somewhat widened dorsally. 43. As in *Calliopsis* s. str. 44. Mesepisternum with area facing anteriorly rather reduced and slightly convex. 45. Preepisternal groove narrow, shallow, punctate, not reaching scrobal level or at least not extending below it. 46. Pterostigma about as long as or longer than and about twice as wide as prestigma (sometimes less than twice); otherwise as in *Calliopsis* s. str. 47. Marginal cell obliquely and broadly truncate, clearly longer than distance from its apex to wing tip. 49. Submarginal cell 1 at least slightly longer than cell 2 + 3. 51. As in

*Calliopsis* s. str. 52. Forewing with cu-v somewhat longer to three times longer than second abscissa M + Cu. 53. Hind wing with cu-v about  $1/4$  as long as second abscissa M + Cu. 54. As in *Calliopsis* s. str. 55. Propodeal triangle finely striate basally. 57. Basitarsus 1 five to nine times longer than broad in male, two to five times in female; tarsomeres moderately widened distally in male. 59. Middle tibial spur with fine, rather sparse teeth; straight and about half as long as (or longer than) basitarsus 2 in female; slightly curved at apex, usually less than half as long as basitarsus 3, in male. 60. Basitarsus 2 of male longer than 1 and about as long as 3; shorter than 1 and 3 in female; male tarsomeres 2-4 widened distally. 61. Tibia 3 of female less than twice as long as basitarsus 3, inner surface with keirotrichia scarce dorsally between patches near ends, absent ventrally; male tibia 3 with keirotrichia on most of inner surface of tibia. 62. As in *Calliopsis* s. str. 63. Hind tibial spurs with fine teeth, inner spur longer than outer; slightly curved at apices. 64. As in *Calliopsis* s. str. 65. Basitarsus 3 unmodified, that of female gradually and slightly tapered toward apex; tarsomeres 2-4 similar to those of tarsi 1 and 2 (although shorter) in male (Fig. 18H), narrower in female. 66, 67, 68. As in *Calliopsis* s. str. 69. T2-5 of male with gradulus posterolaterally short, usually not strongly carinate and postgradular depression shallow, very narrow; posterior marginal areas of T1-5 in male and T1-4 in female pilose; terga (both sexes) with no hair bands; lateral fovea of T2 (both sexes) slightly depressed, narrow in male, much wider in female. 70. Pygidial plate of male long, with well-defined margins. 71. T7 of female with dorsal, proximal area not greatly expanded (Fig. 19B). 72. T8 of male as in Figure 18G. 73. S1-5 of male with hairs dense, mostly directed backward and appressed, usually longer on distal area; S6 with hairs only on distal projections. 73a. S1-5 of female with hairs similar to those of male. 75. S5 of male with a median, narrow, medium-sized projection on distal margin; projection densely pilose at apex (Fig. 18E). 77. S6 of male with distal margin greatly projected medially; projection with small distal emargination (Fig. 18F). 78. S6 of female with proximal laminar lobes sometimes with very shallow emargination between them; basal sclerotization usually spine-shaped [widened at apex in *C. (N.) zonalis* Cresson, tapered in other species], mostly free from sternum; duplication somewhat sclerotized, attached to a distal hardened area of sternum; distal margin produced medially; S6 with distal hairs curved, forming a dense curved band (Fig. 19A). 79. S7 of male distally rectangular, usually distally emarginate and with two short lateral lobes; proximal arms forming a V (Fig. 18D). 80. S8 of male with distal projection elongate, clavate; body of sternum widened medially, with a small, tapered projection at each side of the distal projection (Fig. 18C). 83. Gonocoxites globose,

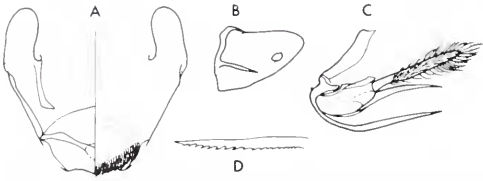


Figure 19. *Calliopsis (Nomadopsis) zonalis* Cresson. Female: A, S6, dorsal and ventral views; B, T7; C, Sting; D, Spur, leg 2.

ventrally connected by membranous area. 85. Volsellae large, connected by slightly sclerotized cuticle, with numerous denticles. 86. Penis valves with some folds, tapered distally, fused dorsally through a rather narrow sclerotized bridge. 87. Penis completely sclerotized except at apex (unlike any other *Calliopsis*, J. Rozen, personal communication), shorter and narrower than valve, clearly separated from valves. 88. See *Calliopsis* s. str. and Figure 19C.

**Comments.** This subgenus contains eight described species (Rozen, 1958). I studied *C. (N.) linsleyi* (Rozen), *puellae* (Cockerell), and *zonalis* Cresson (the first two are new combinations). The females of this subgenus do not present features that distinguish them as a group from *Macronomadopsis* and *Micronomadopsis* (Rozen, 1958).

**Discussion.** Although *Nomadopsis* (usual sense) was confused with *Spinoliella* for a long time, there is no doubt that they belong to two different lineages among the Calliopsini. A similar statement was also made by Shinn (1967). Rozen (1951, 1958) and Shinn (1967) agree about the close relationship among the traditional *Nomadopsis*, *Calliopsis*, *Hypomacrotera*, *Liopoeum* and *Acamptopoeum*, the latter being, in my analyses, a distinct genus, the sister group of *Calliopsis*.

The cladogram (Fig. 30) shows that *Micronomadopsis* is the sister group of *Nomadopsis* s. str. and *Macronomadopsis*. According to Rozen (1958), however, based on male genitalia and S7-8, *Nomadopsis* s. str. "... is quite distinct from *Macronomadopsis* and *Micronomadopsis* and can not be affiliated more closely with one or the other." The male genitalia of *Nomadopsis* resemble those of *Macronomadopsis* (especially in shape of penis valve and volsella), more than those of *Micronomadopsis*. The first two share some apomorphies that indicate that they are more closely related to one another than to *Micronomadopsis*. Furthermore, the shape of the sterna of some *Nomadopsis* s. str. and *Macronomadopsis* is transitional between the two subgenera.

**Distribution.** Western United States, southern British Columbia, and northern México.

### Subgenus *Macronomadopsis* Rozen (Figs. 20, 30)

*Macronomadopsis* Rozen, 1958: 93. Type species: *Nomadopsis micheneri* Rozen, 1958 (original designation).

**Diagnosis.** Differs from *Nomadopsis* as follows: **Male.** Tarsus 1 and 2 with tarsomeres 2-4 conspicuously widened distally. S4 with distal median projection inconspicuous. S5 with median projection on distal margin small, slightly sclerotized.

**Description.** Agrees with description of *Nomadopsis* except: 1. Length 8-12 mm. 3. Pronotum sometimes with no yellow marks. 13. Segment 1 of labial palp somewhat longer than to twice as long as 2-4 together. 16. Maxillary blade longer than prepalpal part of galea. 17. Galeal comb of about 30 bristles. 20. Labrum usually broader than long [about twice as broad as long in *C. (M.) zebra* Cresson]. 27. Clypeus usually more than twice as broad as long [little less than twice as broad in *C. (M.) anthidia* Fowler]; in lateral view protuberant 1/3 to 1/5 width of eye. 31. Subantennal area slightly wider than inner suture length. 34. Antennal socket about middle of face. 37. Lower mesal paraocular area swollen to slightly convex. 38. Facial fovea shallow. 42. Gena of male (lateral view) somewhat narrower than eye, slightly widened dorsally. 45. Pre-

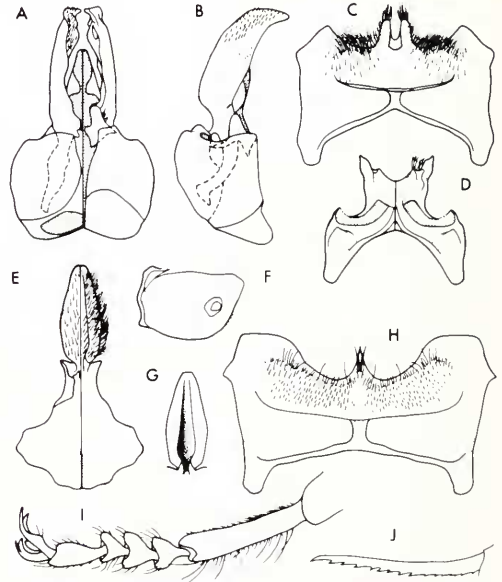


Figure 20. *Calliopsis (Macronomadopsis) zebra* Cresson. Male: A, B, Genitalia, dorsal, ventral and lateral views; C, S6, ventral view; D, E, S7 and 8, dorsal and ventral views; G, S8, distal projection, ventral view (hairs omitted); H, S5, ventral view; I, Tarsus 3. Female: F, T7; J, Spur, leg 2.

episternal groove very short and weak, difficult to see. 46. Pterostigma less than twice as broad as prestigma. 51. First recurrent vein never very close to first transverse cubital. 53. Hind wing with cu-v about 1/3 or 1/4 as long as second abscissa M+Cu. 54. Dorsal surface of propodeum about as long as metanotum. 57. Basitarsus 1 six to seven times longer than broad in male and about four times in female; tarsomeres 2-4 of all tarsi distinctly expanded distally in male, slightly so in female. 59. Middle tibial spur with fine teeth as in *Nomadopsis* but clearly longer than half length of basitarsus 2 in female, about half as long in male. 60. Basitarsus 2 of male shorter than 1 and 3; about as long as 1 and shorter than 3 in female; tarsomeres 2-4 widened distally, more conspicuously so in male than in female. 61. Tibia 3 of female about twice as long as basitarsus 3. 65. Tarsus 3 with tarsomeres 2-4 somewhat expanded distally (Fig. 20I). 71. T7 of female rather square (Fig. 20F). 74. S4 of male inconspicuously produced on distal margin medially. 75. S5 of male with median projection on distal margin small, rather tapered at apex, slightly sclerotized (Fig. 20H). 77. S6 of male with a narrow, median distal emargination and 2 short, mesal projections (Fig. 20C). 78. S6 of female similar to that of *Nomadopsis* but with deep V-shaped emargination between proximal laminar lobes, basal sclerotization spine-like. 79. S7 of male similar to that of *Nomadopsis* but distal margin more deeply emarginated and lateral lobes better defined (Fig. 20D). 80. S8 of male with distal projection narrowed toward apex (Fig. 20E, G). 85. Volsellae connected by slightly sclerotized cuticle, with no denticles. 86. Penis valves strongly curved at apices (Fig. 20A). 87. Penis partially sclerotized, about as wide as valve.

**Comments.** This subgenus contains five species (Rozen, 1958; Hurd, 1979). I studied *C. (Macronomadopsis) micheneri* (Rozen) and *zebrata* Cresson (only *C. zebrata* illustrated) (new combinations).

**Distribution.** United States west of South Dakota, Colorado, and New Mexico (Hurd, 1979).

### Subgenus *Micronomadopsis* Rozen

(Figs. 21, 30)

*Micronomadopsis* Rozen, 1958: 107. Type species: *Nomadopsis fracta* Rozen, 1958 (original designation).

**Diagnosis.** Similar to but usually smaller than *Nomadopsis* and *Macronomadopsis*, from which it differs as follows: *Male*. Tarsus 1 with tarsomeres 2-4 very thin. Tarsus 3, in several species, with tarsomeres 2-4 widened laterally, asymmetrical. Penis valve (in most species) as in Figure 21A. S4 and S5 as in *Nomadopsis*. *Female*. Middle tibial spur with only 4 teeth on distal half.

**Description.** Agrees with description of *Nomadopsis* except: 1. Length 5-10 mm. 8. Head broader than thorax in male, about as broad in female. 11. Glossa somewhat longer than prementum to

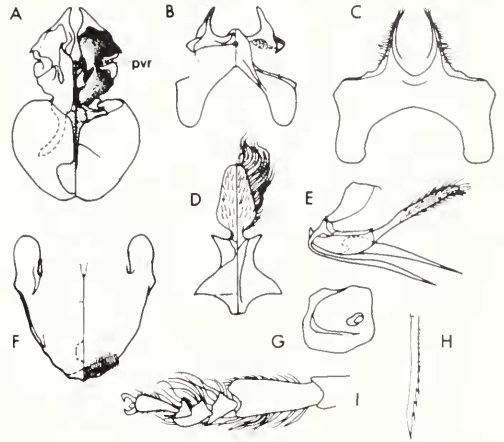


Figure 21. *Calliopsis (Micronomadopsis) scutellaris* Fowler. *Male*: A, Genitalia, dorsal and ventral views; B, S7, dorsal and ventral views; C, S6, ventral view; D, S8, dorsal and ventral views; I, Tarsus 3. *Female*: E, Sting; F, S6, dorsal and ventral views; G, T7; H, Spur, leg 2. pvr = penis valve ridges.

much shorter. 13. Segment 1 of labial palp slightly shorter to about three times longer than 2-4 together. 16. Maxillary blade length as in *Macronomadopsis*. 17. Galeal comb of about 14 bristles. 27. Clypeus sometimes twice as broad as long, protuberant almost 1/3 to 1/7 width of eye. 31. Subantennal area wider than inner suture length, about as wide as socket (sometimes wider). 34. Antennal sockets about middle of face as in *Macronomadopsis*. 36. Antennal flagellum of male as long as head or longer. 42. Gena of male (lateral view) narrower than eye, broadest in the middle. 43. Pronotum similar to that of *Nomadopsis*, although ridge laterally less developed. 45. Pre-episternal groove short, sometimes indistinct. 46. Pterostigma longer than prestigma. 51. First recurrent vein as in *Macronomadopsis*. 52. Forewing with cu-v usually slightly longer than second abscissa M+Cu. 53. Hind wing with cu-v as in *Macronomadopsis*. 54. Dorsal surface of propodeum usually somewhat longer than metanotum, shorter in *C. (Micronomadopsis) helianthi* (Swenk and Cockerell). 55. Propodeal triangle weakly striate, sometimes smooth. 57. Basitarsus 1 six to seven times longer than broad in male, three to four times longer in female; tarsomeres 2-4 unmodified. 59. Middle tibial spur about 1/2 to 1/4 as long as basitarsus 2 in male. 60. Basitarsus 2 of male at least slightly longer than 1, somewhat variable in relation to 3; of female as in *Macronomadopsis*. 61. Tibia of female similar to that of *Nomadopsis* except with keirotichia of inner surface denser dorsally in *C. (M.) helianthi*. 62. Tibial scopa sometimes of hairs with very short branches. 65. Basitarsus 3 unmodified, sometimes very short; tarsomeres 2-4 from un-

modified to widened and asymmetrical in male of several species (Fig. 21I), slender, unmodified in female. 67. Metasoma narrower to slightly wider than thorax. 70. Pygidial plate of male sometimes shorter and wider than in *Nomadopsis* [e.g., in *C. (M.) helianthi*]. 71. T7 of female square (Fig. 21G). 75. S5 of male with distal median projection longer than in *Nomadopsis* (tapered or truncate at apex). 77. S6 of male with distal margin deeply emarginate medially, with two elongate, tapered projections (Fig. 21C). 78. S6 of female similar to that of *Macronomadopsis*. 79. S7 of male with distal area usually with lateral, almost horizontal expansions (Fig. 21B); sometimes with short, median, spine-shaped projection on proximal margin. 80. S8 of male somewhat similar to that of *Macronomadopsis* (Fig. 21D). 85. Volsella similar to that of *Macronomadopsis*. 86. Penis valve complex, similar to that of *Liopoeum*, *Hypomacrotera*, *Calliopsis*, *Perissander*, *Liopoeodes* and *Ceroliopoeum*, with fine, minute ridges laterally (ventral view) as in *Hypomacrotera*, *Calliopsis*, *Perissander*, *Liopoeodes* and *Ceroliopoeum* (Fig. 21A). 87. Penis very short, partially sclerotized, much narrower than valve. 88. Sting as in Figure 21E.

*Comments.* *Micronomadopsis* contains 20 species (Rozen, 1958; Hurd, 1979). I studied *C. (Micronomadopsis) helianthi* (Swenk and Cockerell) [= *euphorbiae* (Cockerell)], *fracta* (Rozen) (new combinations), and *scutellaris* Fowler.

Rozen's (1958) species of uncertain position, *C. boharti* (Rozen), *smithi* (Rozen) and *xenus* (Rozen), were not assigned to any subgenus. Some of their characters fit with *Macronomadopsis* and others with *Micronomadopsis*.

*Distribution.* This subgenus is widespread in the western part of the United States.

### *Liopoeodes*, new subgenus

(Figs. 22, 30)

Type species: *Calliopsis (Liopoeodes) xenopus*, new species (see Appendix).

*Diagnosis.* Similar to *Liopoeum* except: Integument mostly dark. Hairs of head and thorax rather brownish and erect. *Male.* Forewing tip dark as in *Hypomacrotera*. Hind tarsus with all segments modified. *Female.* Black, metasomal terga with apical white hair bands.

*Description.* As in *Liopoeum* except: 1. Length 6–8 mm. 3. Lower half of face (reduced spots) and forelegs of male with yellow marks; female without yellow. 4. Metasoma without yellow areas. 5. Pubescence darkened; on head and thorax mostly erect and clearly longer than that of metasoma. 7. Punctures especially fine and dense on metasomal terga. 14. Segment 2 of labial palp slightly longer than 3. 17. Galeal comb of 23 bristles. 20. Labrum less than twice as broad as long; basal area with distal margin a well marked ridge. 27. Clypeus somewhat protuberant (1/2 to

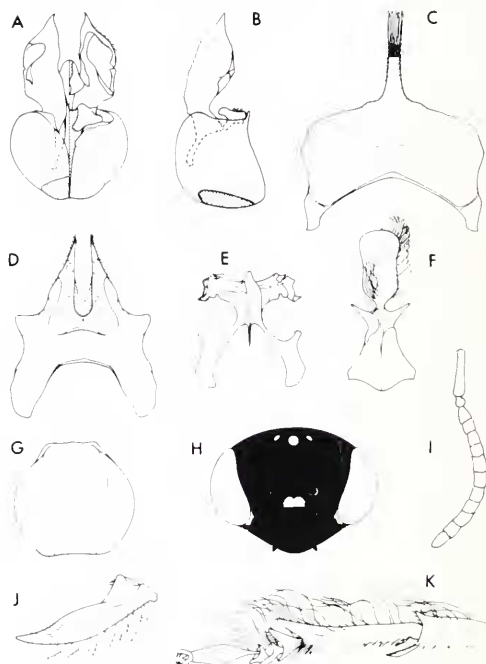


Figure 22. *Calliopsis (Liopoeodes) xenopus* n. sp. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S5; D, S6; E, F, S7 and 8, dorsal and ventral views; G, T8; H, Head, frontal view (hairs omitted); I, Antenna; J, Mandible; K, Tarsus 3.

1/3 width of eye in lateral view); distal margin with well-developed projection near lateral margin of labrum. 34. Antennal socket somewhat below middle of face in both sexes. 36. Antennal flagellum of male with flagellomere 1 slightly longer than broad. 37. Lower paraocular area slightly convex. 38. Facial fovea well defined, longer and broader in female than in male. 42. Gena of male (lateral view) narrower than eye. 46. Pterostigma with margin within marginal cell slightly convex. 49. Submarginal cell 1 somewhat shorter than cell 2+3. 51. First recurrent vein rather close to transverse cubital vein. 53. Hind wing with cu-v about 1/5 as long as second abscissa M+Cu. 55. Propodeal triangle basally microareolate, depressed medially, with fine and weak striae. 57. Basitarsus 1 about seven times longer than broad in male and almost six times in female. 59. Middle tibial spur of female with several well-defined and clearly separated teeth, slightly shorter than basitarsus 2; in male about 1/3 basitarsal length. 60. Basitarsus 2 of male less than twice as long as 1 and 3; basitarsus 2 of female slightly longer than 1 and 3. 61. Tibia 3 of female about twice as long as basitarsus 3, inner surface with keirotrichia at proximal and distal ends and toward upper margin. 63. Hind tibial

spurs with fine teeth, almost straight in male, outer one somewhat curved at apex in female. 64. Basitibial plate of male clearly distinguishable. 65. Basitarsus 3 of male modified distally; tarsomeres 2-4 asymmetrical; distitarsus modified (Fig. 22K). 66. Claws with rather short rami in male, especially on tarsus 3. 69. T1-5 of male and T1-4 of female with posterior marginal areas apparently glabrous; terga of female with distal hair bands; lateral fovea of T2 widened and slightly depressed, almost indistinguishable and ventral in position rather than lateral in male. 70. Pygidial plate of male apparently absent. 71. T7 of female as in Figure 23D. 72. T8 of male as in Figure 22G. 73. S1-5 of male with hairs sparse, mostly on middle line. 75. S5 of male with median projection shorter than in *Liopoeum*; apical hairs of projection longer than in *Liopoeum* (Fig. 22C). 79. S7 of male with tapered projection between proximal arms as in *Hypomacrotera* (Fig. 22E). 80. S8 of male with distal projection somewhat convex ventrally (Fig. 22F). 83. Gonocoxites, in dorsal view, without mesal proximal projection. 85. Volsellae with no denticles. 88. Sting rather short, not reaching stylus apex (Fig. 23C).

**Comments.** The subgenus *Liopoeodes* contains a single species from Argentina. The subgeneric name is slightly modified from one used by J. S. Moure on some 30-year-old identification labels found in the collection of the Snow Entomological Museum (KU).

**Discussion.** The mosaic of features exhibited by this new subgenus (some of them also present in other calliopsine genera) is one more evidence that it and its close relatives should be treated as species of the genus *Calliopsis*.

The presence of a darkened area at the apex of the forewing of the male suggests *C. (Hypomac-*

*rotera*) and some species of *C. (Perissander)*. On the other hand, because of other characters indicated above, *Liopoeodes* appears to be more like *C. (Liopoeum)*.

**Etymology.** The name of this subgenus is based on *Liopoeum* plus the Greek suffix *-odes*, indicating similarity to *Liopoeum*.

### *Ceroliopoeum*, new subgenus

(Figs. 2D, 24, 30)

Type species: *Camptopoeum laetum* Vachal, 1909.

**Diagnosis.** Appearance similar to that of *Liopoeum* but clypeus convex medially and with marginal projection (beside labrum) broadly rounded; labrum with distal margin of basal part a strong ridge, almost a carina; pubescence short and rather sparse. **Male.** Antennal scape stout. Basitarsus 2 very narrow, longer than basitarsus 3 (at least slightly). Tarsus 3 with tarsomeres 2-4 narrow, apices not expanded laterally. **Female.** Tibial spur 2 as long as basitarsus 2, sinuate, with small, well-separated teeth.

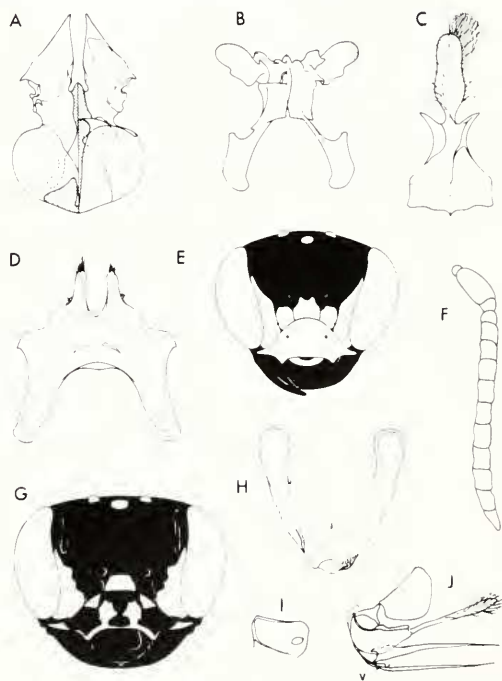


Figure 24. *Calliopsis (Ceroliopoeum) laeta* (Vachal). **Male:** A, Genitalia, dorsal and ventral views; B, C, S7 and 8, dorsal and ventral views; D, S6, ventral view; E, Head, frontal view; F, Antenna. **Female:** G, Head, frontal view; H, S6, dorsal and ventral views; I, T7; J, Sting. v = valve-like structure.

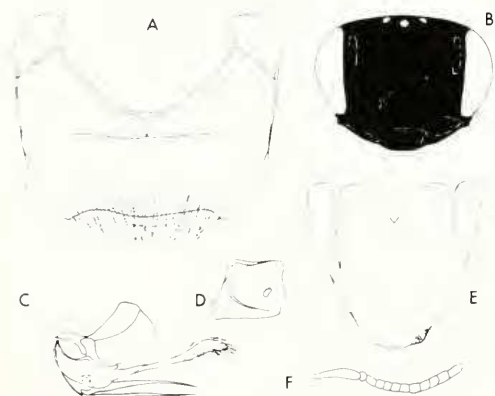


Figure 23. *Calliopsis (Liopoeodes) xenopous* n. sp. **Female:** A, S5, ventral view; B, Head, frontal view (hairs omitted); C, Sting; D, T7; E, S6, dorsal and ventral views; F, Antenna.

*Description.* Agrees with that of *Liopocum* except: 1. Length 5-6 mm. 3. Male with legs mostly yellow; female with yellow spots on pronotum (as in male), tibiae and tarsi. 5. Pubescence rather short, mostly very short and appressed on metasoma. 8. Head about as wide as thorax. 17. Galeal comb of 12 bristles. 20. Labrum with distal margin of basal part a strong ridge, almost a carina; apical area flattened. 27. Clypeus somewhat protuberant (1/3 width of eye in lateral view), with distal margin (frontal view beside labrum) broadly rounded; central area convex. 34. Male with flagellomere 1 about half as long as 2. 35. Antennal scape robust. 38. Facial fovea narrow, well delimited. 42. Gena of male (lateral view) about 1/2 as wide as eye. 46. Pterostigma somewhat more than twice as broad as prestigma; margin within marginal cell slightly convex. 52. Forewing with cu-v about as long as second abscissa of M+Cu. 55. Propodeal triangle microareolate, depressed medially and with very fine longitudinal striae. 57. Basitarsus 1 almost eight times longer than broad in male, about six times in female. 59. Middle tibial spur of female as long as basitarsus 2, sinuose, with fine, well-separated teeth. 60. Basitarsus 2 about as long as 1 and slightly longer than 3 in male, and about as long as 1 and 3 in female. 61. Tibia 3 of female on inner surface with keirotrichia dense at proximal and distal ends, sparser toward dorsal margin. 62. Tibial scopa of sparse and minutely branched hairs. 65. Tarsus 3 unmodified. 67. Metasoma in male narrower than thorax. 69. T1-5 of male and T1-4 of female with posterior marginal area scarcely pilose; hairs somewhat denser on T4 of female; lateral fovea of T2 (both sexes) indistinguishable. 70. Pygidial plate of male clearly delimited laterally, rather truncate at apex. 71. T7 of female as in Figure 24I. 73a. S1-5 of female with hairs sparser than in *Liopocum* and *Acampopocum* and mostly not appressed. 75. S5 of male with median projection tapered apically (as in Fig. 11G). 79. S7 of male with patch of small, sparse hairs medially on latero-distal projections (Fig. 24B). 80. S8 of male with distal projection convex ventrally (Fig. 24C). 83. Gonocoxites, in dorsal view, without proximal mesal projection. 85. Volsella without denticles. 88. First valvula of sting with a minute expanded area, perhaps a rudiment of valve, and a very short, curved hair behind this structure (Fig. 24J).

*Comments.* *C. (Ceroliopocum) laeta* (Vachal) is the only known species of this subgenus.

*Discussion.* In the cladogram (Fig. 30), *Ceroliopocum* is the sister group of *Hypomacrotera*, *Liopocum*, *Nomadopsis*, *Macronomadopsis* and *Micronomadopsis* together.

*Distribution.* Argentina.

*Etymology.* The name of the subgenus refers to the distinctive antennal flagellum and the likeness to *Liopocum*. It is from the Greek *keras*, horned, plus *Liopocum*.

### Genus *Arhysosage* Brèthes

(Figs. 6C, 8C, 25, 26, 30)

*Arhysosage* Brèthes, 1922: 121. Type species: *Arhysosage johnsoni* Brèthes, 1922 = *Camptopocum ochraceum* Friese, 1908 (monobasic).

*Ruiziella* Timberlake, 1952: 105 (preoccupied). Type species: *Camptopocum ochraceum* Friese, 1908.

*Ruziapis* Timberlake, 1952: 528 (*lapsus* for *Ruizapis*, and replacement for *Ruiziella*).

*Ruizapis* Timberlake, 1953: 598 (emendation of *Ruziapis*).

*Diagnosis.* Related to *Spinoliella* and *Callonychium*, sharing with them the low position of the antennal sockets. It can be differentiated by the following characters: Orbits distinctly divergent below. Hind tibial spurs distinctly curved toward apices. *Male.* Body almost completely yellow. Mandible strongly curved and elongate, with preapical tooth and projection on upper margin.

*Description.* 1. Length about 10 mm. 3. Most of head and thorax of male yellow; size of yellow areas of female variable. 4. Metasoma with yellow bands very extensive to largely incomplete. 5. Pubescence in general short; appressed hairs on most of dorsum of thorax and metasoma. 7. Punctures very fine and dense. 8. Head broader than long and broader than thorax. 11. Glossa longer than prementum, slender. 12. Paraglossa shorter than suspensorium. 13. Segment 1 of

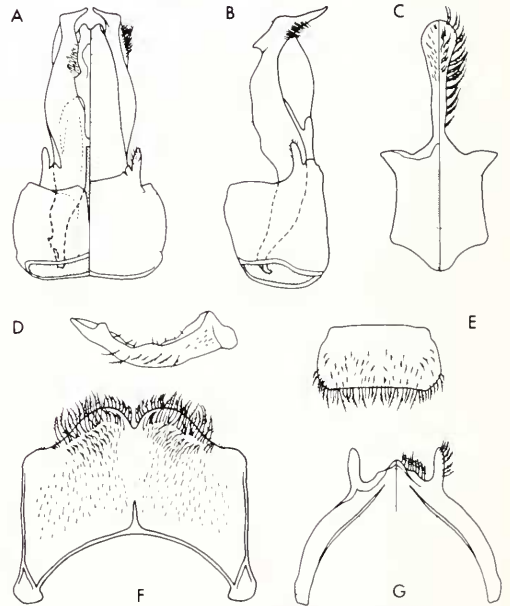


Figure 25. *Arhysosage ochracea* Brèthes. Male: A, B, Genitalia, dorsal, ventral and lateral views; C, S8, dorsal and ventral views; D, Mandible; E, Labrum; F, S6, ventral view; G, S7, dorsal and ventral views.

labial palp less than twice as long as 2-4 together. 16. Maxillary blade longer than prepalpal part of galea. 17. Galeal comb absent. 20. Labrum less than twice as broad as long, partially or fully pilose; flat in male, with slight transverse ridge (almost flat) in female. 25. Mandible of male strongly arcuate, upper margin with prebasal projection and also with preapical tooth (sometimes very conspicuous) (Figs. 6C, 25D). 27. Clypeus more than four times broader than long and somewhat protuberant ( $1/3$  width of eye, lateral view) in male; about three times broader than long and distinctly protuberant (about  $1/2$  width of eye, lateral view) in female; distal margin with distinct projection (variable in size) near lateral margin of labrum. 30. Inner subantennal suture angulate. 31. Subantennal area wider than length of inner suture and than antennal socket. 33. Tentorial pit almost at middle of outer subantennal suture. 34. Antennal socket far below middle of face (on lower third in male, somewhat higher in female). 36. Antennal flagellum of male unmodified, much shorter than head; flagellomere 1 about as long as 2 or little longer and about as long as broad. 37. Lower mesal paraocular area slightly convex. 38. Facial fovea deep, narrow. 39. Orbits strongly divergent below in male, slightly so in female. 40. Middle ocellus below dorsal orbital tangent, lateral ocelli above. 41. Vertex convex. 42. Gena of male (lateral view) wider than eye, slightly wider dorsally than ventrally. 43. Pronotum with dorsal preapical ridge rounded, strong in male, weak in female. 44. Mesepisternum with flattened area facing anteriorly rather reduced. 45. Pre-episternal groove only distinguishable above scrobal level, continued downward as black line (difficult to see on dark integument). 46. Pterostigma longer than and slightly wider than prestigma; side basal to vein r subparallel to costa, that within marginal cell straight. 47. Marginal cell obliquely and broadly truncate at apex, longer than distance from apex to wing tip (slightly so in female). 49. Submarginal cell 1 about as long as cell 2 + 3 or longer. 51. First recurrent vein clearly distant from first transverse cubital. 52. Forewing with cu-v as long as or longer than second abscissa M + Cu. 53. Hind wing with cu-v little less than  $1/2$  to  $1/3$  as long as second abscissa M + Cu. 54. Dorsal surface of propodeum slightly longer than metanotum. 55. Propodeal triangle basally with fine striae, depressed medially. 57. Basitarsus 1 about five times longer than broad in male and four times longer in female; tarsomeres 2-4 unmodified. 59. Middle tibial spur about half as long as basitarsus 2 or somewhat longer, distinctly curved apically, finally serrate (apical teeth larger than those at base). 60. Basitarsus 2 about as long as 1 and shorter than 3, tarsomeres 2-4 unmodified. 61. Hind tibia of female somewhat longer than basitarsus 3; inner surface with keirotrichia in patch at base and apex, sparse or absent toward dorsal margin, absent ventrally

(Fig. 26C); male tibia 3 with keirotrichia on most of inner surface but sparser ventrally. 62. Tibial scopa of moderately dense and apparently simple, but minutely branched hairs. 63. Hind tibial spurs strongly curved toward apices, outer about as long as inner or somewhat longer; teeth small. 64. Basitibial plate of male with margins well defined. 65. Tarsus 3 unmodified. 66. Claws deeply cleft, rami subequal in male, inner ramus much shorter than outer in female. 67. Metasoma in male wider than thorax. 69. T<sub>2</sub>-5 of male with gradulus posterolaterally long (surpassing middle of each tergum), strongly carinate (especially on T<sub>2</sub>-4) and with postgradular depression narrow, rather shallow; posterior marginal areas of T<sub>1</sub>-5 in male and T<sub>1</sub>-4 in female pilose (minute hairs); terga (both sexes) with no hair bands; lateral fovea of T<sub>2</sub> (both sexes) slightly depressed, small in male, larger in female. 70. Pygidial plate of male well developed, abruptly elevated and carinate laterally on distal part, apex slightly emarginate. 71. T<sub>7</sub> of female not expanded dorsally but with a strong ventral proximal projection (Fig. 26D). 72. T<sub>8</sub> of male hexagonal (Fig. 26F). 73. S<sub>1</sub>-6 of male with most of hairs minute, dense, appressed, and directed posteriorly, longer distally. 73a. S<sub>1</sub>-5 of female pilose as in male but hairs somewhat longer and denser. 74, 75. S<sub>4</sub> and 5 of male with distal margins slightly and broadly concave medially. 77. S<sub>6</sub> of male distally bilobed, with small median V-shaped emargination (Fig. 25F). 78. S<sub>6</sub> of female with basal spine-like sclerotization fused to sternum; lateral margin with strong curved ridge; duplication thin, attached to distal hardened area of sternum; distal margin concave medially; S<sub>6</sub> apically with a well-defined, curved and dense band of curved hairs (Fig. 26B). 79. S<sub>7</sub> of male distally with 2 rather short, finger-like lateral projections; proximal arms long and forming a U (Fig. 25G). 80. S<sub>8</sub> of male with a median long distal projection clavate at apex, abruptly separated from basal part which has weak median ridge dorsally (Fig. 25C). 83. Gonocoxite short, squared, completely fused both dorsally and ventrally (Fig. 25A, B). 84. Gonostylus short, finger-like, fused to gonocoxite. 85. Volsella apparently absent? (or completely fused to gonocoxite). 86. Penis valves long, with some folds, distally bent downward at right angle, tapered toward apex, dorsally fused to each other by small, narrow bridge. 87. Penis almost reaching apices of penis valves, proximally wider and fused to valve; distal half well sclerotized ventrally. 88. Sting very short (not attaining stylus apex) (Fig. 26E).

*Comments.* This genus contains three known species: *A. flava* Moure, *\*germana* Moure, *\*ochracea* (Friese).

*Discussion.* *Arhysosage* is, according to the cladogram (Fig. 30), the sister group of *Spinoliella* and *Callonychium*.

*Distribution.* Argentina.

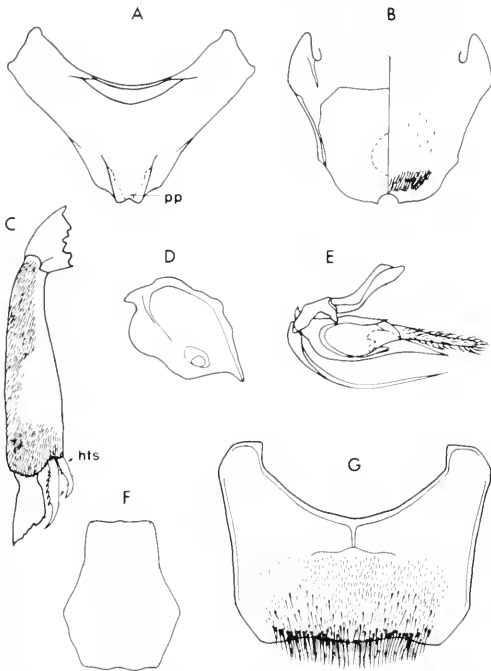


Figure 26. *Arhysosage ochracea* Brèthes. *Male*: A, T7, dorsal view; F, T8. *Female*: B, S6, dorsal and ventral views; C, Tibia 3, inner view; D, T7; E, Sting; G, S5, ventral view. hts = hind tibial spurs; pp = pygidial plate.

**Genus *Spinoliella* Ashmead**  
(Figs. 7A, 27, 28, 30)

**Diagnosis.** Closer to *Callonychium* than to *Arhysosage*. It can be differentiated from *Callonychium* as follows: Gena black. Antennal sockets on lower third of face or nearly so. Clypeus with lateral part (beside mandibular articulation) rather horizontal. *Male*. Basitibial plate a swollen and shiny area, not delimited by carina. *Female*. S6 narrowed and with patch of hairs distally. Sting short, not reaching stylus.

**Description.** 1. Length 4–9 mm. 3. Lower part of face (below antennal socket) and some areas of legs with yellow marks. Thorax black (sometimes with small yellow spots). 4. Metasomal terga with yellow laterally or forming bands. 5. Pubescence short, especially short and appressed on metasoma. 7. Punctures in general fine. 8. Head broader than long and as broad as thorax or nearly so. 11. Glossa approximately as long as prementum or longer. 13. Segment 1 of labial palp about twice as long as 2–4 together, or somewhat longer. 16. Maxillary blade about twice as long as prepalpal part of galea. 17. Galeal comb of about 14–17 bristles. 20. Labrum less than twice as broad as long; basal part glabrous;

distal margin of basal area a weak transverse ridge; labral apex flattened (Fig. 27D). 25. Mandible with well-developed, pointed, basal projection on upper margin [mandible strongly curved in male of *S. nomadooides* (Spinola)] (Fig. 27F). 27. Clypeus variable in width (in males more than three to five times broader than long, in females less than three to four times broader); distinctly protuberant (lateral view); distal margin with strong projection near lateral margin of labrum. 30. Inner subantennal suture angulate or strongly curved. 31. Subantennal area slightly wider than inner suture length and than antennal socket. 33. Tentorial pit approximately at midpoint of outer subantennal suture. 34. Antennal socket on lower third of face or nearly so. 36. Antennal flagellum of male unmodified, much shorter than head; flagellomere 1 about as long as 2 or little longer, and slightly longer than broad. 37. Lower paraocular area strongly swollen mesally. 38. Facial fovea narrow, well marked. 39. Orbits subparallel or slightly divergent below. 40. Middle ocellus below dorsal orbital tangent. 41. Vertex convex. 42. Gena of male (lateral view) generally wider than eye (about as wide as eye in *S. psamita* Toro and Ruz), of uniform width or somewhat wider in the middle. 43. Pronotum with dorsal preapical ridge usually more prominent laterally than medially. 44. Mesepisternum with surface facing anteriorly extremely reduced and slightly convex. 45. Pre-episternal groove weak, almost reaching

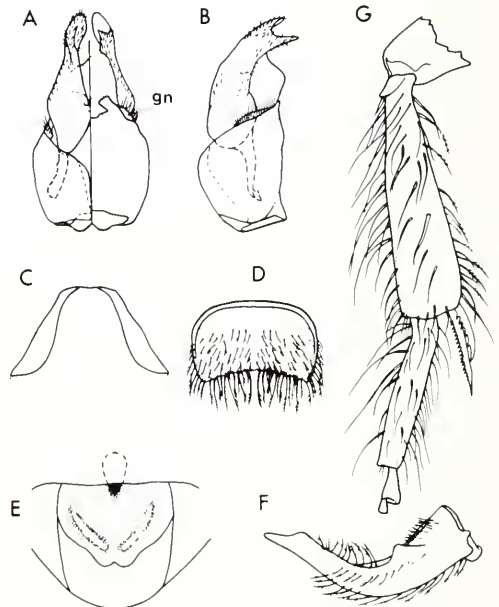


Figure 27. *Spinoliella nomadooides* (Spinola). *Male*: A, B, Genitalia, dorsal, ventral and lateral views; C, T8; D, Labrum; E, Metasomal tip showing S6; F, Mandible. *Female*: G, Leg 3, outer view. gn = gonostylus.



scrobal level. 46. Pterostigma longer than (at least slightly) and somewhat less than twice as wide as prestigma; side basal to vein r subparallel to costa, that within marginal cell straight or nearly so. 47. Marginal cell rather widely and somewhat obliquely truncate at apex, variable in length. 49. Submarginal cell 1 longer than cell 2 + 3. 51. First recurrent vein distant from first transverse cubital. 52. Forewing with cu-v longer than second abscissa M + Cu. 53. Hind wing with cu-v less than 1/2 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum at least twice as long as metanotum. 55. Propodeal triangle basally depressed medially, microareolate, with no striae, glabrous. 57. Basitarsus 1 about seven times longer than broad in male, five times longer in female; tarsomeres 2-4 unmodified. 59. Middle tibial spur almost straight, finally serrate; usually about half as long as basitarsus 2 (sometimes somewhat longer). 60. Basitarsus 2 usually as long as 1 (sometimes somewhat longer) and shorter than 3, tarsomeres 2-4 unmodified. 61. Tibia 3 of female (Figs. 27G, 28D) almost twice as long as basitarsus 3; keirotrichia on inner surface forming patches at both ends (sometimes with few hairs between patches); male tibia 3 with keirotrichia rather dense but absent medially. 62. Tibial scopa of medium-sized, simple, sparse hairs (especially on outer surface). 63. Inner hind tibial spur with fine and dense teeth, almost straight; outer with teeth sparser than on inner. 64. Basitibial plate of male a swollen shiny area without defined margins; in female, rounded with margin a weak ridge. 65. Basitarsus 3 of female and tarsomeres unmodified. 66. Claws (in both sexes) bifurcate as in *Arhysosage*. 67. Metasoma in male usually slightly narrower than thorax. 69. T2-5 of male with gradulus posterolaterally short, not strongly carinate and with postgradular depression narrow (about 1/10 length of tergum) and shallow except somewhat deeper on T2; posterior marginal areas of T1-5 in male and T1-4 in female pilose; terga (both sexes) with no hair bands; lateral fovea of T2 (both sexes) slightly depressed, usually oval, somewhat variable in size. 70. Pygidial plate of male well developed with margins carinate. 71. T7 of female trapezoidal (Fig. 28C) or squared. 72. T8 of male as in Figure 27C. 73. Metasomal sterna of male with hairs mostly very short, more abundant laterally, sparse or absent on midline, directed posteriorly (some directed obliquely on S6). 73a. Metasomal sterna of female with hairs short, dense, directed caudad, not appressed, longer only on distal sternal margins. 74, 75. Similar to *Arhysosage*. 77. S6 of male with distal margin produced medially (Fig. 27E). 78. S6 of female with proximal laminar lobes surpassing the apodemes; duplication thin (attached to hardened area of sternum distally); S6 with distal margin medially produced or concave; with pre-marginal fringe or patch of hairs at apex (Fig. 28E). 79. S7 of male distally with two small

projections; proximal arms forming a V (Fig. 28B). 80. S8 of male with body gradually separated from median distal projection; projection tapered toward apex and short-pilose (Fig. 28A). 83. Gonocoxites rather elongate, though somewhat wider in middle except *S. psamita*, rather squared (seen from ventral side); ventrally completely fused on midline. 84. Gonostylus vestigial (about 1/8 length of gonocoxite in ventral view) and fused to gonocoxite (Fig. 27A, B). 85. Volsellae indistinct, apparently absent (perhaps represented only by sclerotized area fused to gonocoxite and gonostylus). 86. Penis valve apically bilobed (simple in undescribed Argentine species not placed as to subgenus). 87. Penis completely membranous, somewhat shorter and wider than valve, and fused to valves basally. 88. Sting short (not reaching stylus apex) (Fig. 28F).

*Discussion.* In the cladogram (Fig. 30) *Spinoliella* is the sister of *Callionychium*; it has few unique apomorphies.

The subgenera *Spinoliella* s. str. and *Peniella* Toro and Ruz are not redescribed here. A key to these two subgenera, however, is given mainly to note some additional characters that separate them and to correct a mistake in the key by Toro and Ruz (1972).

#### KEY TO THE SUBGENERA OF *SPINOLIELLA*

1. Males . . . . . 2
- Females . . . . . 3
2. Basitarsus 3 on outer surface with hairs short, dense. Facial fovea at least as

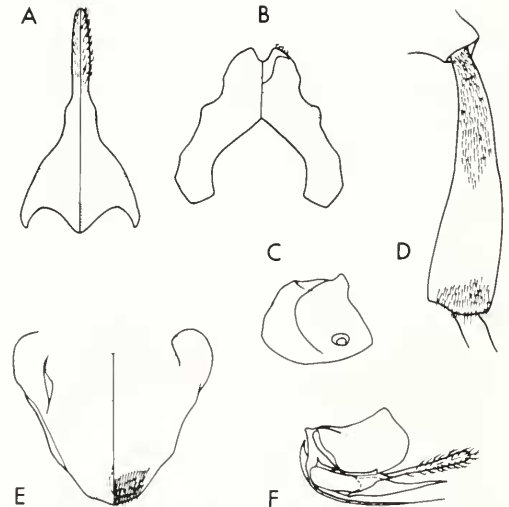


Figure 28. *Spinoliella nomadoides* (Spinola). Male: A, B, S8 and 7, dorsal and ventral views. Female: C, T7; D, Tibia 3, inner view; E, S6, dorsal and ventral views; F, Sting.

- broad as one-third minimum width of scape. S6 with distal projection gradually separated from rest of sternum and noticeably surpassing lateral areas . . . . . *Spinoliella* s. str.
- Basitarsus 3 on outer surface with hairs long, sparse. Facial fovea approximately as broad as one-fifth minimum width of scape. S6 with distal projection rather abruptly separated from rest of sternum and slightly surpassing lateral areas . . . . . *Peniella*
3. Outer hind tibial spur about half length of inner, distinctly curved at apex (Fig. 27G). S6 distally much narrower than proximally; hairs at apex dense, forming a patch at each side of midline . . . . . *Spinoliella* s. str.
- Outer hind tibial spur about 2/3 length of inner, almost straight. S6 with distal area slightly narrower than proximally; hairs at apex ordered in 3 well-defined rounded rows . . . . . *Peniella*

#### Subgenus *Spinoliella* Ashmead s. str.

*Spinoliella* Ashmead, 1899: 84. Type species: *Camp-topocum nomioides* (sic) Spinola = *Camp-topocum nomadoides* Spinola, 1851 (monobasic and original designation).

This subgenus is easily distinguished by the characters given in the above key and in Toro and Ruz (1972).

*Comments.* *Spinoliella* s. str. contains two species: \**S. (S.) nomadoides* (Spinola) and \**psamita* Toro and Ruz.

*Distribution.* Chile.

#### Subgenus *Peniella* Toro and Ruz

*Peniella* Toro and Ruz, 1972: 146. Type species: *Camp-topocum maculatum* Spinola, 1851 (original designation).

This subgenus is distinguished by the characters given in the above key and by Toro and Ruz (1972).

*Comments.* *Peniella* includes four species: *S. (P.) \*maculata* (Spinola), \**herbsti* (Friese), \**rozeni* Toro and Ruz and \**rufiventris* Toro and Ruz.

*Distribution.* Chile.

#### Genus *Callonychium* Brèthes

(Figs. 6D, 7B, 8D, 29, 30)

*Diagnosis.* Close to *Spinoliella*, distinguished as follows: Gena with yellow. Antennal sockets (lower margins) usually at lower fourth of face. Lateral part of clypeus strongly bent posteriorly. *Male.* Basitibial plate flattened, delimited by car-

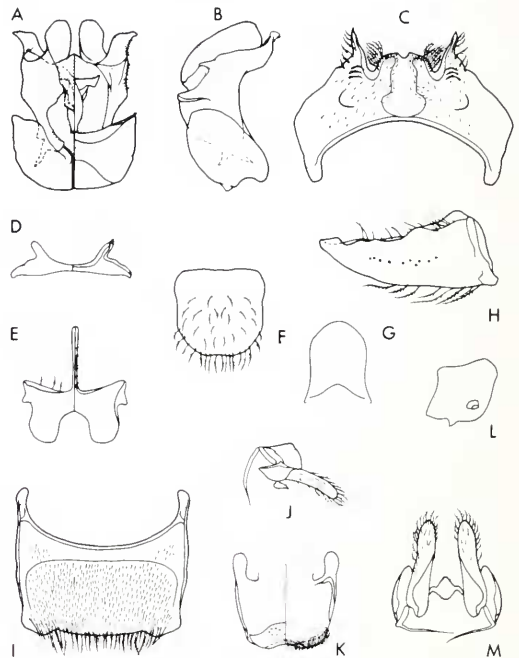


Figure 29. *Callonychium mandibulare* Brèthes. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S6, ventral view; D, E, S7 and 8, dorsal and ventral views; F, Labrum; G, T8; H, Mandible. *Female:* I, S5, ventral view; J, Sting, lateral view; K, S6, dorsal and ventral views; L, T7; M, Sting, ventral view.

ina. Metasomal apex strongly bent down and forward. Sterna with modifications (ridges, projections, carinae). *Female.* S6 distally almost as broad as basally, distal margin slightly concave with curved distal band of curved and dense hairs.

*Description.* 1. Length 3–7 mm. 3. Head and thorax with several to extensive yellow areas, more abundant in male than in female. Yellow area of lower part of face generally prolonged onto dorsal part along orbit, yellow also on gena. Thorax with yellow at least on pronotum, metanotum and legs. 4. Metasoma with yellow marks laterally only or forming complete or fragmented bands. 5. Pubescence short and sparse on head and thorax, shorter and appressed on metasoma. 6. Integument in general distinctly microareolate, especially on head and thorax, slightly so on metasoma. 7. Punctures mostly fine, sparse on head and thorax, smaller on metasoma except on sterna of male, dense on sterna of female. 8. Head somewhat broader than long and usually about as broad as thorax. 11. Glossa about as long as prementum or longer. 13. Segment 1 of labial palp almost three times longer than 2–4 together

or longer. 16. Maxillary blade about twice as long as prepupal part of galea. 17. Galeal comb absent. 20. Labrum about as long as broad or broader; basal area glabrous; distal margin of basal area in male usually appearing flattened or with weak ridge, of female with ridge stronger than in male; labral apex not inflexed in either sex. 25. Mandible of male with moderate to strong process on upper margin. 27. Clypeal width variable (almost three to five times broader than long), usually distinctly protuberant (about 1/3 of eye width in lateral view), lateral part strongly bent posteriorly, distal margin usually with no projection near lateral margin of labrum. 28. Epistomal suture, below intersection of outer subantennal suture, usually almost straight. 30. Inner subantennal suture angulate just below antennal socket (Fig. 6D). 31. Subantennal area wider than inner suture length and wider (or much wider) than socket. 33. Tentorial pit at midpoint of outer subantennal suture or nearly so. 34. Antennal sockets (lower margins) usually at lower fourth of face (sometimes at lower third). 36. Antennal flagellum of male unmodified, much shorter than head; flagellomere 1 as long as 2 or longer, about as long as broad. 37. Lower mesal paraocular area often conspicuously protuberant; lateral part of lower paraocular area strongly bent posteriorly. 38. Facial fovea well marked, narrow (almost linear). 39. Orbits generally subparallel, sometimes slightly convergent below in male. 40. Ocelli variable in position (middle ocellus above or below dorsal orbital tangent). 41. Vertex convex. 42. Gena of male (lateral view) somewhat variable in width, of uniform width from above to below or somewhat wider medially. 43. Pronotum with dorsal preapical ridge prominent only laterally (weak or absent medially). 44. Mesepisternum with area facing anteriorly usually reduced and slightly convex. 45. Pre-episternal groove shallow, appearing only as a line (as in *Arhysosage*) if extending below scrobal level. 46. Pterostigma longer than and about twice as wide as prestigma; side basal to vein r subparallel to costa [except clearly divergent in *C. mandibulare* (Friese)], that within marginal cell straight. 47. Marginal cell obliquely and widely truncate at apex, shorter than distance from its apex to wing tip. 48. Submarginal cells two. 49. Submarginal cell 1 longer than cell 2 + 3. 51. First recurrent vein entering 2nd submarginal cell but variable in position, not meeting first transverse cubital. 52. Vein cu-v shorter than second abscissa M + Cu. 53. Hind wing with vein cu-v 1/4 to 1/6 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum usually about twice as long as metanotum or longer. 55. Propodeal triangle basally with no special modifications, glabrous. 57. Basitarsus 1 five to seven times longer than broad in male and four to seven in female; tarsomeres 2-4 unmodified. 59. Middle tibial spur somewhat curved, finely toothed and about half as long as basitarsus 2 or nearly so. 60. Basitarsus 2 longer than basitarsus 1 (at least

slightly) and shorter than 3. 61. Tibia 3 of female about twice as long as basitarsus 3 or nearly so; inner surface with keirotrichia limited to patch at each end; male tibia 3 with keirotrichia forming narrow band of sparse hairs on inner surface between patches at ends. 62. Tibial scopa of medium or small, scattered and inconspicuously branched hairs on outer surface; longer and denser on dorsal margin. 63. Hind tibial spurs appearing untoothed but with minute teeth difficult to see; outer shorter than inner, slightly curved or almost straight, inner straight. 64. Basitibial plate of male well defined, sometimes with smooth borders. 65. Tarsus 3 unmodified. 66. Claws deeply cleft with rami subequal in male, simple in female. 67. Metasoma in male narrower than thorax (except about as broad as thorax in *C. mandibulare* Friese). 69. T2-5 of male with gradulus posterolaterally short (weak) or absent and postgradular depression narrow, shallow, except deep on T2 of *C. mandibulare*; posterior marginal areas of T1-5 in male and T1-4 in female pilose; terga (both sexes) without hair bands; lateral fovea of T2 (both sexes) with shape, length and depth variable. 70. Pygidial plate of male well developed, rounded or bifurcate at apex. 71. T7 of female rather squared, with dorsal and proximal area not greatly expanded (Fig. 29L). 72. T8 of male somewhat variable but usually similar to an elongated trapezoid (Fig. 29G). 73. S1-5 of male with hairs mostly directed posteriorly, variable in length and density, mostly short, somewhat oblique on S6; sternal surface with modifications such as protuberances, projections, ridges or carinate areas; metasoma strongly curved down and forward at apex. 73a. S1-5 of female with hairs mostly short, dense, appressed. 74. S4 of male with distal margin almost straight, somewhat concave or emarginate (except widely convex in *C. mandibulare*). 75. S5 of male with distal margin almost straight medially (except widely convex in *C. mandibulare*). 76. S5 of female with long and recurved gradulus and no median sclerotized area between gradulus and proximal margin (Fig. 29I). 77. S6 of male distally with emargination (deep or shallow) between lateral and median areas (Fig. 29C). 78. S6 of female with proximal laminar lobes widely separated from lateral apodemes; basal sclerotization absent; lateral margin with strong, somewhat curved ridge; duplication heavily sclerotized; distal margin concave medially with dense curved hairs (Fig. 29K). 79. S7 of male transverse, bar-like, with a short laterodistal projection (Fig. 29D). 80. S8 of male with elongate, slender, median projection abruptly separated from a proximally emarginate rectangular body (Fig. 29E). 83. Gonocoxites short, rather square, ventral and dorsal sides completely fused. 84. Gonostylus rudimentary, fused to gonocoxite (recognizable only by the few, small hairs). 85. Volsellae indistinct, apparently absent (or represented only by a sclerotized transverse area completely fused to each other and to gonocoxite). 86.

Penis valves usually complex; dorsally, not attached to each other by bridge but attached basally to penis by membrane. 87. Penis membranous (variable in shape), shorter and wider than valve, with special internal sclerotization. 88. Sting rudimentary (reduced to a small sclerotized area), triangular plate modified, elongate (Fig. 29J, M).

*Comments.* The subgenera *Callonychium* Brèthes and *Paranychium* Toro recognized by Toro (1989) have not been redescribed in this study, although a key for subgenera by Toro and Herrera (1980) is here provided. The type species of this genus, *C. argentinum*, was not available for study.

*Discussion.* *Callonychium* is clearly differentiated by its apomorphies and is more closely related to *Spinoliella* than to *Arhysoyage*. The relationship among these three genera has been also noted by Toro and Herrera (1980).

Rozen (personal communication) has studied the larvae of *Spinoliella herbsti* and a new species of *Callonychium*. His preliminary observations indicate that both species present "peculiar thoracic tubercles . . ." that "may represent a synapomorphy." He has also found that the low antennal papillae of most panurgines are somewhat or strongly projecting in these species; they are presumably synapomorphic. On the other hand he stated that "the recessed labial maxillary region of *Callonychium* and the projecting one of *Spinoliella* seem incongruous with the idea of the close relationship."

In my opinion the first two characters indicated by Rozen are likely to be good synapomorphies, which would reinforce the close cladistic relationship indicated by adult characters between *Spinoliella* and *Callonychium*. The third character, however, may not be useful to establish relationships.

The similarity between the flabellum of *Callonychium* and that of *Perdita* that Michener and Brooks (1984) observed does not lead to the conclusion that these two genera are closely related, and as those authors concluded, must result from convergence.

KEY TO THE SUBGENERA OF *CALLONYCHIUM*

- 1. Axilla yellow, acute. First metasomal sternum of male without premarginal process . . . . . *Callonychium* s. str.
- Axilla black, depressed. First metasomal sternum of male with premarginal process . . . . . *Paranychium*

**Subgenus *Callonychium* Brèthes s. str.**

*Callonychium* Brèthes, 1922: 120. Type species: *Callo-*

*nychium argentinum* Brèthes, 1922 (monobasic).

This subgenus is distinguished by the characters given in Toro and Herrera (1980).

*Comments.* The subgenus *Callonychium* s. str. contains six species: *C. argentinum* Brèthes, *brasiliense* (Ducke), *\*flaviventre* (Friese), *luteimaculatum* (Strand), *\*mandibulare* (Friese) and *petunia* Cure and Wittmann and others (undescribed) from eastern South America.

*Distribution.* Argentina, Paraguay, Brazil.

**Subgenus *Paranychium* Toro**

*Paranychium* Toro and Herrera, 1980: 213 (not valid because no type species was designated).

*Paranychium* Toro, 1989: 231. Type species: *Camptopocum chilense* Friese, 1906 (original designation).

This subgenus is distinguished by the characters given by Toro and Herrera (1980) and by Toro (1989).

*Comments.* The subgenus *Paranychium* contains five species: *C. (P.) \*chilense* (Friese), *\*aricensis* Toro and Herrera, *\*atacamense* Toro and Herrera, *\*coquimbense* Toro and Herrera and *minutum* (Friese) as well as undescribed species from Argentina.

*Distribution.* Argentina, Chile.

CLADISTIC ANALYSIS

This is part of a larger study of the subfamily Panurginae. A preliminary hypothesis of relationships among genera of Panurginae was used to identify the close relatives of the three tribes Perditini, Protomeliturgini, and Calliopsini (Ruz, 1986). The tribe Meliturgini was regarded as the sister to the three tribes mentioned above, and these four were in turn related to the tribe Panurgini. This outgroup information was used to construct a hypothetical ancestor using the Maddison, Donoghue and Maddison algorithm (1984). This ancestor is characterized in the matrix (Table 2) and its characters were coded according to codes for the entire subfamily. Thus "1" may be apomorphic at the subfamily level, but plesiomorphic at the present level of analysis. This was done so that the several studies I plan (including Ruz, 1986) can be examined together.

When a character is variable within a taxon, the code for the plesiomorphic state (0) was used in the analysis. An exception was character 72 (Fig. 30) for which the derived state in *C. (Micronomadopsis)* was used to demonstrate an apparent convergence with *C. (Liopoeodes)*. Omission of character 72 did not change the topology of the cladogram.

Table 1. List of characters for genera and subgenera of panurgine tribes Calliopsini, Protomeliturgini and Perditiini. (For the Panurginae as a whole, (0) is considered plesiomorphic but for the groups treated here it is in a few cases apomorphic.)

3. *Metasoma with yellow markings* (1). Although the presence of yellow on the metasoma is widespread among bees, including some genera of Panurginae, it is lacking almost completely in the outgroups, which indicates that its presence should be considered as apomorphic. Lack of yellow was coded (0).

5. *Metasomal terga with distal hair bands* (1). Several groups of bees exhibit this feature, which apparently has arisen independently in different lineages. Among the Panurginae, however, it is present only in *Protomeliturga*, *Acamptopoeum*, *Calliopsis* s. str., *C. (Perissander)*, *C. (Calliopsima)*, and *C. (Verbenapis)*. Since this character is also present in various Andreninae and colletid bees (both outgroups) it is possible that the lack of these hair bands (coded 0) is not plesiomorphic but is apomorphic. The genera of Panurginae mentioned above, however, because of other sets of characters, are considered among the most derived genera. Therefore the presence of these hair bands is likely to be apomorphic.

6. *Glossa more or less as long as prementum* (1). This condition was considered as apomorphic for the subfamily, since a shorter glossa (0) is present in most genera of the Andreninae and Colletinae. This study, however, shows that this condition (1) may be present in the ancestor of Calliopsini and is widespread among the Calliopsini and other Panurgini; it therefore is considered as a plesiomorphy for Calliopsini.

*Glossa shorter than prementum* (coded as 0 in Table 2) is an apomorphy for the present analysis and appears as a reversal in the cladogram (Fig. 30) for *C. (Perissander)* and *Perdita* (although the glossa is long in some groups of *Perdita*).

8. *Paraglossa shorter than suspensorium* (1). An autapomorphy for *Arhysosage*, a highly derived genus. Although the paraglossa is short in Andreninae (outgroup), this feature seems to be autapomorphic for *Arhysosage*, a genus with many derived characters. In other Panurginae the paraglossa is longer than or about as long as the suspensorium (0), and for this subfamily this condition is presumably plesiomorphic. Both shortness of the paraglossa in *Arhysosage* and its strong elongation among the long-tongued bees seem to be apomorphic.

9. *Segment 2 of labial palpus about three times longer than 3* (1). Autapomorphic, unique for *Protomeliturga*. Segment 2 of the labial palpus in other Panurginae and in the outgroups is usually about as long as 3, or if longer, less than two times longer than segment 3 (0).

11. *Segments 3-4 of labial palpus articulating preapically and projecting at about 90° to the axis of 1-2* (1). An autapomorphy for *Protomeliturga*, unique among the short-tongued bees, in almost all of which the articulation of the labial palpal segments 2-4 is apical (0). The preapical articulation between labial palpal segments 2 and 3 is present in long-tongued bees and is certainly derived.

12. *Mentum about 1/5 length of prementum* (1). A few Panurginae present the apomorphic condition: *Callonychium* and two Old World genera, *Camptopoeum* and *Melitturga*. Short-tongued bees usually have a mentum shorter to much shorter than 1/5 the length of the prementum, a condition which is plesiomorphic and coded (0).

13. *Galeal comb absent* (1). Many Panurginae and the outgroups have a well-developed galeal comb (0). This comb is absent in *Arhysosage*, *Callonychium* (also in some *Perdita*) and in several Old World panurgines. The evolutionary trend goes from comb well developed, reduced, to absent; the later condition is clearly derived.

15. *Labrum of male with weak transverse ridge* (1). *Labrum of male flat* (2). One or the other of the derived states of this character appears occasionally among Panurginae. A weak ridge is present in *Spinoliella* and *Callonychium*, while a flat labrum characterizes some Old World and North American genera, and *Arhysosage*. A labral ridge (sometimes strong) or carina (delimiting the basal area) (0) is widespread among bees including the outgroups except in *Megandrena* (Andreninae) in which the labrum is flat, without a ridge.

16. *Labrum of male with basal area pilose* (1). Generally when a labral ridge or carina exists, hairs appear lateral and distal to the ridge or carina. This is also the case among many Panurginae and in the outgroups. The genera that present the derived feature are indicated in the cladogram, except for *Perdita* in which only some species have developed the derived condition. Lack of such hairs is coded (0).

17. *Labrum of female with apex not inflexed* (1). Among females of Panurginae and the outgroups, this feature is present only in *Arhysosage*, *Spinoliella*, and *Callonychium*. Otherwise the female labrum usually

shows the plesiomorphic condition, that is, with the apex at least slightly inflexed (0).

18. *Mandible of male simple* (1). This is an apomorphic character for the Panurginae since nearly all colletids and most Andreninae have bidentate mandibles. Among the Calliopsini, a *preapical tooth* is present only in *Arhysosage*. This condition (coded as 0 in Table 2) also appears in many Perditiini and should be considered as apomorphic for the tribes here considered. The cladogram shows this as a reversal in *Perdita* and *Arhysosage*.

22. *Tentorial pit of male at intersection of outer subantennal and epistomal sutures* (1). *Tentorial pit of male in outer subantennal suture (close to epistomal suture)* (2). *Tentorial pit of male near middle of outer subantennal suture* (3). In colletids (second outgroup for Panurginae), even though they possess only the inner subantennal suture, the tentorial pit is in the epistomal suture sometimes considerably below the subantennal suture (0). In Andreninae (first outgroup for Panurginae) this pit is sometimes in the intersection between the epistomal and the outer subantennal suture, as in (1). The migration of the tentorial pit into the outer subantennal suture is unique to Panurginae and obviously apomorphic. Condition (1) should be considered plesiomorphic in this study, while (2) and (3) are sequential apomorphic states and uniquely derived characters in the Calliopsini.

23. *Antennal sockets of male (lower margins) on lower 1/3 or 1/4 of face* (1). In most Panurginae and outgroups the antennal sockets are placed more or less in the middle of the face (0).

24. *Antennal scape of male robust* (1). Apomorphy for some Old World genera and *Calliopsis* (*Ceroliopocum*). A derived feature among Panurginae, absent in the outgroups. A slender scape is coded (0).

28. *Lower paraocular area strongly swollen mesally* (1). This character is rarely present among bees. The only Panurginae with this feature are *Spinoliella* and *Callonychium*, although it is approached in some *Calliopsis* and *Perdita*. The rest of the genera have the lower paraocular area flattened or slightly convex (0). In the outgroups this area is usually completely flat.

37. *Pronotal carina or lamella of male present* (1). This structure is present only in three genera of Panurginae, one of which is *Protomeliturga*, although it seems that it appears independently in several other groups of bees. Many bees, including the panurgine outgroups, show the plesiomorphic condition, i.e., the lack of a carina or lamella on the dorsal part of pronotum (0); instead, at least laterally, a rounded ridge is developed.

39. *Pre-episternal groove short, not extending below scrobal level* (1). A short pre-episternal groove is present in all the tribe Calliopsini, in some other panurgine genera and some Andreninae. The Colletinae (second outgroup), however, show a very long groove that always extends below the scrobe (0). This fact indicates that a long groove is plesiomorphic and a short one apomorphic.

40. *Pre-episternal groove curved, meeting scrobe* (1). Some Andreninae and *Perdita* and *Acamptopocum* among the Panurginae present this feature, which is clearly apomorphic. In Colletinae the pre-episternal groove is straight and does not meet the scrobe (0), which indicates that this is the primitive condition. In Andrenidae as a whole the scrobal suture is absent in front of the scrobe. Therefore it is unlikely that the lower part of the curved groove noted above is derived from the scrobal suture, although this is the usual interpretation.

41. *Axilla of male with patch of velvety hairs* (1). The presence of this feature is a unique apomorphy for *Calliopsis* s. str.; it is unknown in other bees. Lack of such hairs is coded (0).

42. *Metanotum with lateral patch of short velvety hairs* (1). This character, known only in *Calliopsis* s. str., *C. (Perissander)* and *C. (Calliopsima)*, must be an apomorphy. Hairs in this area usually are not different than on the rest of the thoracic dorsum (0). In *Calliopsis* s. str. the patch is conspicuous and brown in males, small and white in females; the latter condition is also present in both sexes of *C. (Perissander)* and *C. (Calliopsima)*.

44. *Pterostigma with sides parallel or subparallel* (1). Among Panurginae this character appears in the whole tribe Calliopsini and independently in a few other genera. Although this character is also present in some genera of the outgroups, it should be considered an apomorphic, since in Panurginae, the Calliopsini are the most derived bees. Pterostigma with margin basal to vein r divergent from costa so that the stigma is relatively broad is the plesiomorphy (0).

45. *Pterostigma with margin within marginal cell straight or nearly so* (1). All the Calliopsini present this apomorphy, although it has also appeared independently in two unrelated genera. Most genera of the outgroups show the plesiomorphy, that is, pterostigma with margin within marginal cell clearly convex (0).

46. *Marginal cell shorter than distance between its apex and wing tip* (1). *Marginal cell much shorter than distance between its apex and wing tip* (2). Most Panurginae and also the outgroups have a marginal cell about as

long as or usually longer than the distance between its apex and the wing tip (0); this is the plesiomorphic condition.

49. *Basal vein (fore wing) strongly curved toward wing base* (1). A unique character for *Protomeliturga*; among Panurginae and the outgroups this vein is usually straight or slightly curved (0).

52. *Propodeal triangle smooth* (1). Only a few genera of Panurginae (all of them Calliopsini) possess this derived character. These are: *Acamptopoeum*, *C. (Verbenapis)*, *C. (Hypomacrotera)* and some *C. (Micronomadopsis)*. Usually the propodeal triangle is striate or rugose, or at least minutely areolate (0). This plesiomorphy occurs in Andreninae and in many Colletinae.

55. *Tarsus 1 of female on inner surface mainly with hairs rigid, curved at apices* (Fig. 14H) (1). A strong, unique character of *Calliopsis (Verbenapis)*. Hairs on this part of the tarsus 1 are rigid but straight (0) in other genera and in the outgroups.

56. *Femur 2 of female with well-defined basal comb on ventral margin* (Fig. 10D) (1). A uniform comb clearly differentiated from the hairs of the surrounding parts of the femur is present in all Calliopsini and, although appearing independently, in a few other genera of Panurginae. The comb of femur 2 of the female in the outgroups consists of stiff, short, dense, but irregularly organized hairs not very different from those of the surrounding areas (0); this must be the primitive condition.

58. *Basitarsus 2 of male longer than 3* (1). This feature is present only in the Calliopsini [*Acamptopoeum*, *Calliopsis* s. str., *C. (Perissander)*, *C. (Liopoeodes)*, *C. (Ceroliopoeum)*, and several *C. (Micronomadopsis)*] and in the Old World genus *Plesiopanurgus*. In the rest of the Panurginae and in the outgroups basitarsus 2 of the male is equal to or shorter than 3 (0).

60. *Tarsus 2 of male with tarsomeres 2-4 widened distally* (1). This feature is found in a few genera of Panurginae and in *Euhrbstia* and *Orphana* (slightly so in the latter) among Andreninae. Rather narrow tarsomeres (0) are plesiomorphic.

62. *Tibia 3 of female on inner surface with keirotichia forming a longitudinal dorsal or medial strip* (1). *Tibia 3 of female with keirotichia only at both ends of inner surface* (Fig. 28D) (2). This sequence seems to represent an evolutionary trend. The lack of keirotichia should be the most derived condition. Presence of keirotichia on most of the inner surface of tibia 3 (0) as in the outgroups is the primitive condition.

63. *Tibia 3 of male with keirotichia forming a longitudinal strip* (1). The keirotichia in many bees are present on most of the inner surface of tibia 3 (0) and (1) should be considered an apomorphy. Reduction to a strip of keirotichia occurs only in *Spinolella*, *Callonychium*, and one Old World genus.

64. *Tibia 3 of male with dorsal margin evenly carinate* (Fig. 4F) or *the carina fragmented, forming a series of teeth* (1). This character appears in several members of the Panurginae but not in its outgroups. For this reason the presence of a tibial carina or of teeth may be apomorphic for the subfamily while its absence (0) is plesiomorphic. In this study, however, the ancestor probably had this feature; therefore the lack of teeth on the tibia 3 of the male in all Calliopsini should be interpreted as apomorphy. State (1) is present in *Protomeliturga* and exceptionally in *Perdita*.

67. *Tibial scopa of moderately abundant hairs* (1). *Tibial scopa of extremely sparse hairs* (2). The scopa is dense (0) in most Andreninae and Colletinae and for that reason at the subfamily level this feature is a plesiomorphy. Among the Calliopsini, however, condition (1) is the most widespread and may have been present in their ancestor: in this analysis, therefore, it is considered a plesiomorphy for Calliopsini. In this tribe only *Spinoliella* and *Callonychium* have the tibial scopa of sparse hairs (2), a derived state. A dense scopa (coded as 0 in Table 2) appears in the cladogram as a reversal for *Perdita*, *Calliopsima*, and *Verbenapis* and should be considered as apomorphic for the tribes here studied.

69. *Basitibial plate of male represented only by a swollen area, laterally not delimited by a ridge or carina* (1). This feature is known only in *Spinoliella* and some *Perdita*; in other panurgines and in most members of the outgroups the plate is delimited (0).

70. *Apex of basitarsus 3 of female with upper distal projection reduced so that apex is oblique* (1). *Apex of basitarsus of female transverse* (2). A well-developed upper distal projection on basitarsus 3 (0) is widespread among bees. Both well-developed and reduced projections are also present in the outgroups of Panurginae. Thus it is difficult to determine the polarity. However, a truncated basitarsus occurs only in some of the otherwise most derived Panurginae, such as *Spinoliella*, *Arhysosage*, *Callonychium* and some *Perdita*. Therefore for Panurginae the direction of evolution is indicated.

70a. *Basitarsus 3 of male expanded laterally at apex on ventral margin* (1), an autapomorphy for *C. (Liopoeodes)* (Fig. 22K). Lack of such expansion was coded (0).

71. *Tarsus 3 of male with tarsomeres 2-4 widened* (1). This character has appeared in three different lineages among the Panurginae and is obviously apomorphic. Unmodified tarsomeres (0) are commonly found in many groups of bees including most genera of the outgroups.

72. *Tarsus 3 of male with tarsomeres 2-4 asymmetrical* (1). Tarsomeres are usually symmetrical (0), a condition widespread in bees and wasps. Among panurgines, asymmetry, a unique and strong character, has been found only in some *Calliopsis* (*Micronomadopsis*), in *C. (Liopoeodes)* and slightly so in some *C. (Liopoeum)*.

72a. *Distitarsus 3 of male widened medially*, (1), a unique character known only for *C. (Liopoeodes)*. In others the distitarsus is widest apically (0).

73. *Claws of female simple* (1). Among Panurginae this character is present only in a few Old World genera and in *Callonychium*. Bifurcate claws (0) are widespread among bees and are obviously plesiomorphic.

76. *T1-5 of male with posterior marginal areas (at least partially) pilose* (1). This feature appears several times among Panurginae and other bees, and may be apomorphic. Since the metasomal terga in the outgroups present either condition, it is difficult to determine the direction of evolution of this character. However, the majority of the presumably more primitive Panurginae have terga with bare posterior marginal areas (0), a condition that may well be plesiomorphic. All genera with metasomal hair bands (character 5) have densely pilose posterior marginal areas.

79. *Pygidial plate of male well defined* (1). A pygidial plate clearly delimited by a ridge or carina is present in most Calliopsini and independently also in a few Old World Panurginae, all of them quite derived genera as shown by other characters. This structure in males is widespread among bees and wasps and is plesiomorphic for the whole group. In Panurginae, however, it seems to be apomorphic, the plate having been largely lost in ancestors of Panurginae. In most genera of the outgroups the plate is represented only by a bare, shiny, triangular area or by an expansion of tergum 7 (0) similar to that of the most primitive Panurginae. This last condition is considered plesiomorphic for Panurginae. Reacquisition of the defined plate should be no great evolutionary problem since the plate is defined in females; appropriate genes only need to be turned on in males.

80. *T8 of male at apex rather densely pilose* (1). Usually T8 has sparse hairs or is glabrous (0). However, in some Panurginae, like *Perdita*, T8 is clearly pilose, a condition not found in the outgroups.

81. *S4 of male with distal margin slightly produced medially* (1), as in *C. (Macronomadopsis)* and *C. (Verbenapis)*, although barely distinct in the latter. *S4 of male with distal margin clearly produced medially* (2). This character is evidently apomorphic, for it is known only in *Calliopsis* and the Old World genus *Plesiopanurgus*, in which it must have arisen independently. S4 in other groups, including the outgroups, usually has the distal margin concave or almost straight medially (0).

84. *S5 of male with distal margin slightly produced medially* (1). *S5 of male on distal margin with a rather small median projection* (2). *S5 of male distally with an elongate median projection* (3). This feature is present only in the genus *Calliopsis*. The margin of S5 is concave or almost straight medially (0) in most bees and wasps; this condition is plesiomorphic.

85. *S1-5 of female with hairs mostly appressed* (1). Several Calliopsini and also *Protomeliturga* and one Old World genus exhibit this character. Although this feature arose independently several times in bees, including the outgroups, it is likely to be an apomorphy in Panurginae since it is present only in otherwise derived genera. *Sterna* with hairs mostly not appressed (0) seems to be the plesiomorphy.

87. *S5 of female with distal margin convex medially* (1). This is a unique and strong synapomorphy of Calliopsini. The rest of Panurginae and outgroups present the plesiomorphic condition, that is, S5 with distal margin concave or almost straight medially (0). This condition is also widespread in other bees and wasps.

88. *S5 of female with median sclerotized area between gradulus and proximal margin of sternum* (Fig. 12A) (1). This derived character is present in Calliopsini and it has also appeared independently in one Old World genus. (In *Callonychium* it is absent, presumably secondarily lost.) The lack of this sclerotization (0) is widespread in bees.

89. *S6 of male with distal, elongate, tapered projection on each side of deep emargination* (Fig. 11H) (1). This structure has arisen only in some Calliopsini. The lack of such projections on S6 (0) is widespread in bees and plesiomorphic.

90. *S6 of male about three or more times broader than long* (1). This strong, derived character is present only in *Perdita*. Usually S6 of the male is about as wide as or somewhat wider than long (0). The outgroups of Panurginae and many other bees possess this plesiomorphic condition.

93. *S6 of female with two proximal laminar lobes* (Fig. 17H) (1). This character is found only in Calliopsini. Without doubt an excellent apomorphy, this structure is unknown in other bees or wasps which have the proximal margin of S6 in females straight (0).

94. *S6 of female without basal sclerotization* (1). This is an autapomorphic character of *Callonychium*. The



presence of basal sclerotization (0) is characteristic of the rest of Panurginae and outgroups.

95. *S6 of female with basal spine-shaped longitudinal sclerotization* (Fig. 1D) (1). This feature is present in most Calliopsini except *Callonychium*. It has also arisen, no doubt independently, in a few other genera of the subfamily. A basal sclerotization of S6 (females) is not spine-shaped (0) in panurgine outgroups; therefore the acquisition of this shape is clearly derived.

96. *S6 of female with basal sclerotization free at least at apex* (1). A basal sclerotization on S6 is usually fused to the sternum (0). Therefore, when the sclerotization has a free apex, it seems clear that this condition is apomorphic.

97. *S6 of female with strong, almost straight ridge on lateral margin* (Fig. 1D) (1). The Calliopsini (except *Arhysosage*), *Perdita*, and some Old World genera possess this character, which is lacking in the outgroups. A lateral ridge on S6, if present, is usually curved (0), a condition which is here considered plesiomorphic.

99. *S6 of female with premarginal hairs in well-organized rows forming a continuous or medially interrupted patch or band* (Figs. 10H, 12C) (1). This unique, strong character appears only in all Calliopsini. Premarginal hairs on S6 are usually organized in a dense patch (0). This primitive condition is present in Andreninae and Colletinae.

102. *S7 of male reduced to a transverse bar with two small latero-distal projections* (Fig. 29D) (1). This unique apomorphy is known only in *Callonychium*. Usually S7 is more conspicuous and of a different shape, commonly v-shaped (0).

103. *S7 of male with small brush of hairs near middle of each lateral projection* (Fig. 15D) (1). This sternal brush is only found in *Calliopsis* (*Liopoeum*); its absence is coded (0).

105. *S8 of male with a small lateral projection between body and distal projection* (Fig. 11F) (1). This strong character appears only in *Calliopsis* except for *C. (Verbenapis)* in which it exists only as two weak lateral bumps. It is absent (0) in other bees.

108. *S8 of male robust, strongly concave laterally* (Fig. 4G, H) (1). This is a unique, strong feature, present only in *Protomeliturga*. A thin structure with unmodified lateral margins is the plesiomorphy (0).

111. *Gonocoxites (ventral view) connected by membrane* (Fig. 18A) (1). *Gonocoxites partially or fully fused to each other* (Fig. 25A) (2). The gonocoxites are completely separated (except at the very bases) (0) in the presumably most primitive Panurginae and in the outgroups as well. Therefore this feature must be a plesiomorphy. The evolution of this character seems to be toward a full fusion of the gonocoxites.

113. *Gonocoxite (dorsal view) proximally with well-developed, mesal, usually lobe-like process* (Fig. 15A) (1). This strong character is present in *Calliopsis* (*Liopoeum*) and in one species of *C. (Hypomacrotera)*. This structure is always lacking (0) in the outgroups.

115. *Gonostylus about 1/2 to 1/3 length of gonocoxite (ventral view)* (1). *Gonostylus vestigial, about 1/8 length of gonocoxite* (2). *Gonostylus rudimentary (recognizable only by the presence of few, short hairs at apex of gonocoxite)* (3). *Gonostylus absent* (4). Reduction in gonostylar length occurs in a few Old World Panurginae as well as in *Protomeliturga* and Calliopsini (almost lost in *Callonychium*). This strong character is rather rare in other groups of bees and lacking in the outgroups. *Gonostylus longer than gonocoxite* (0) is the ancestral condition.

118. *Volsella rudimentary or absent (?)* (1). Most Panurginae, all Andreninae and Colletinae have well-developed volsellae (0). *Arhysosage*, *Spinoliella*, and *Callonychium* are the only Panurginae that have apparently lost them.

119. *Volsellae connected to one another by basal, narrow and weak, membranous bridge* (1). *Volsellae connected to one another by widened membranous area or by slightly sclerotized cuticle* (2). *Volsellae partially fused to one another* (3). *Volsellae fully fused to one another but line of fusion visible* (4). *Volsellae absent or completely fused forming a highly sclerotized plate*, coded as missing (9) for *Arhysosage*, *Spinoliella* and *Callonychium*. In the outgroups and many other bees the volsellae are free from one another (0). They may be attached to the gonocoxites or penis valves but not to each other. *Volsellae mesally free* is certainly a plesiomorphy.

120. *Volsellae without denticles* (1). Denticles are usually present (0) on the volsellae. In *Protomeliturga* and some Calliopsini, however, the teeth are lost.

122. *Penis valve (lateral view) with longitudinal row of hairs* (1). This autapomorphy for *Acamptopoeum* is absent in the outgroups, which lack such hairs (0).

123. *Penis valve complex* (1). The presence of complex folds in the penis valve is found only in some subgenera of *Calliopsis*. Most primitive Panurginae and the outgroups possess simple penis valve (0).

125. *Penis completely separated from penis valve* (1). Most Panurginae and outgroups possess a penis partially or fully fused to the penis valve (0). In *Acamptopoeum* and *Calliopsis*, however, these structures are completely separated.

126. *Penis with internal sclerotization* (1). An internal sclerotization of the penis is a rare feature in other bees and is totally absent (0) in the outgroups. It is found only in *Spinoliella* and *Callonychium*.

127. *Sting short to very short, not reaching (or at least not surpassing) stylus* (1). *Sting rudimentary* (2). Females of many bees and wasps have a long sting which is commonly exposed. This is true in colletids and some Andreninae. In Panurginae, only the most primitive ones have an elongate sting (0), which may be seen from outside but less frequently than that of Colletinae. A short sting is present in most Calliopsini (except *Acamptopoeum*), *Protomeliturga*, *Perdita*, and in a few Old World genera. It is rudimentary, no doubt the most derived condition, in *Callonychium*.

128. *Sting truncate at apex* (1). This strong feature is present only in *Acamptopoeum* and some *Perdita* (e.g., *P. halictoides*). Commonly the sting is acute at the apex (0). An apically truncate sting must mean that, even if it is elongate, it cannot be used for introducing venom.

129. *First valvifer elongate* (1). The first valvifer (triangular plate) is usually more or less triangular (0). In *Perdita* and independently in *Callonychium*, however, the first valvifer is elongate, a modification probably related to reduction of the sting. This clearly derived condition is not found in Colletinae and is rare in Andreninae.

130. *Valve of first valvula rudimentary* (Fig. 24J) (1). *Valve absent* (Fig. 16B) (2). A well-developed valve of the first valvula (0) is present when there is a long sting, as in Colletinae and some Andreninae. The tendency in evolution is toward the loss of the valve, which is correlated with the weak sclerotization of the first valvula. In *Protomeliturga*, *Perdita*, a few Old World genera, and most Calliopsini there is no valve. A tiny projection that may be a valve rudiment is present in *C. (Ceroliopoeum)* and some Old World genera. In this study the absence of a valve in the three tribes involved should be interpreted as a plesiomorphic character and the presence of a valve-like structure in *Ceroliopoeum*, as an autapomorphy.

Seventeen taxa (15 taxa used by Ruz, 1986, and 2 additional taxa, *Liopoeodes* and *Ceroliopoeum*) and a total of 52 characters have been used in this study (Tables 1 and 2). Of the 130 derived characters previously considered (Ruz, 1986) for the whole subfamily, 53 were eliminated for being invariant among, or not applying to, the taxa here involved. Besides, 17 autapomorphies plus characters 70a and 72a added later, five convergences (see Table 1), and three characters with consistency indices (C.I.) 0.250 or below, were not used in this cladistic analysis. The three characters eliminated were the following: 26, Flagellomere 1 of male about twice as long as 2 or less. Even though this feature is diagnostic for some genera, it appears independently several times among Panurginae. 100, S6 of female with curved band of hairs on premarginal area. This character is known only in Calliopsini and seems to be derived, but it appears to arise independently and to reverse several times within the tribe. 116, Gonostylus partially or fully fused to gonocoxite. The gonostylus is lacking in several genera and subgenera of Calliopsini. Therefore this character was not informative in this study.

The presence of hair bands on the metasomal terga (character 5) was only considered as a character for males. In several taxa among the Calliopsini these hair bands are present in both sexes. In *Calliopsis* (*Liopoeodes*), however, they are present only in females. The C.I. of this character of females was too low to be considered in the analysis.

The polarity of variables (sequence of character

states within each variable) has been determined using outgroup comparison. The outgroups considered for the entire subfamily are: Andreninae (the other subfamily of Andrenidae) and Colletinae (the subfamily considered the most primitive among Colletidae).

The data (Table 2) were analyzed using a computer program (Swofford, 1985, PAUP version 2.4) based on parsimony. The options selected were the following: 1. MULPARS. 2. Rooting. 3. Global branch-swapping. 4. Delayed transformation optimization. Only three most parsimonious trees were found, which showed almost no topological differences. Therefore only one tree (Fig. 30) is illustrated. Statistics of the tree: length = 115; C.I. = 0.6.

The cladistic analysis of the data in Table 2 indicated that Calliopsini is a strong monophyletic group, some of its synapomorphies being unique among all bees. It also shows that this tribe is subdivided into two clearly differentiated lineages, and that the sister group of *Acamptopoeum* is also well supported.

The relationships among the nine taxa at the top of the tree, however, do not seem to be very stable due to homoplasies. Moreover, some taxa or groups of taxa are differentiated by reversals only. *Calliopsis* s. str. and *Perissander*, the sister group of the remaining seven taxa, may appear in a trichotomy depending on the distribution of character 42. This character may arise earlier in the cladogram (as a synapomorphy for all the nine taxa plus *Calliopsima*) and be reversed later



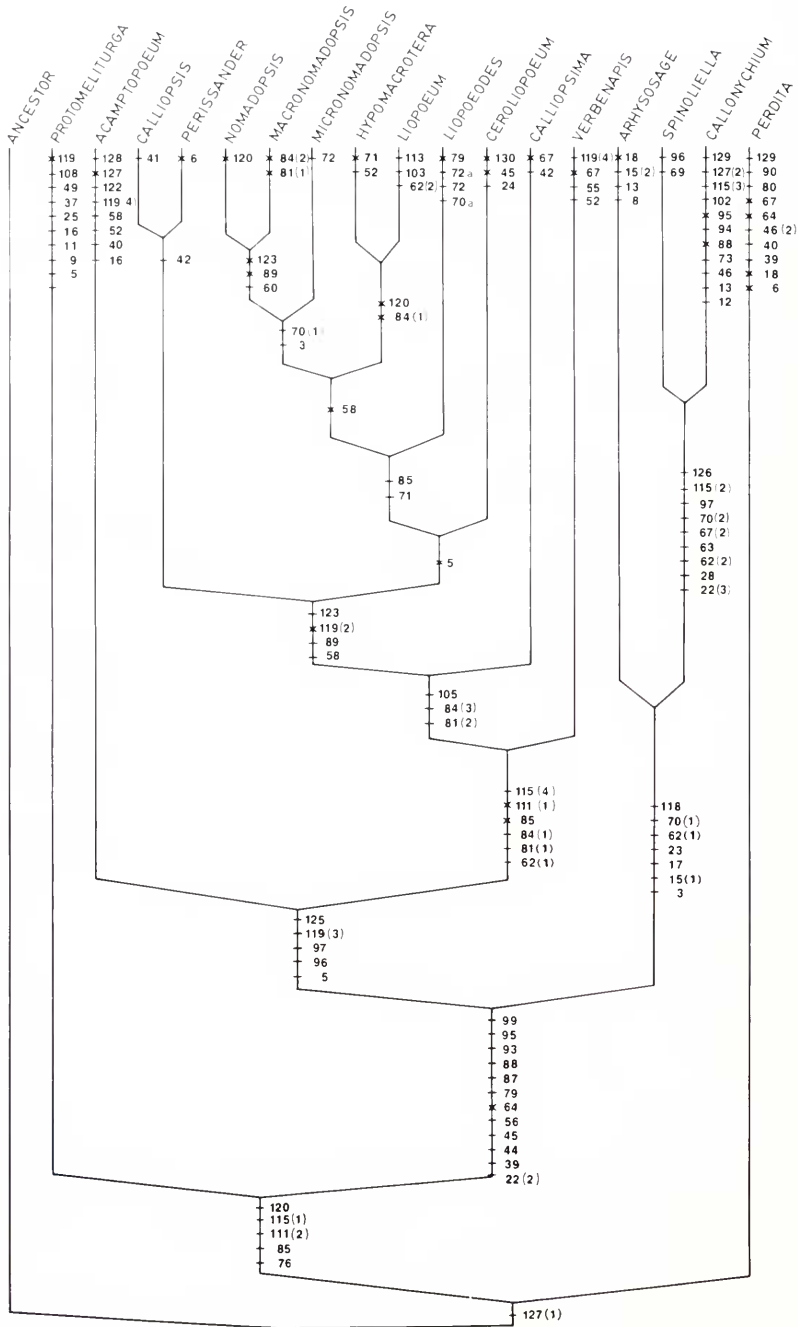


Figure 30. Cladogram showing the phylogenetic relationships of the genera and subgenera of the tribes Perditiini, Protomeliturgini and Calliopsini. Autapomorphies and convergences (see Table 1) are also included here but only data in Table 2 were used in cladogram construction.

for the seven taxa mentioned above. On the other hand, if the characters eliminated (see above: 26, 100, 116) are maintained, some of the trees show *Acanthopocum* as the sister group of the whole tribe, although there are only two characters that would support this arrangement.

The subgenera of *Spinoliella* and *Callonychium* agree in all characters shown in Table 2 and therefore were not segregated in the cladistic

analysis.

The two outgroups of the Calliopsini, *Protomeliturga* and *Perdita*, were considered here to show how they relate to the tribe Calliopsini. A preliminary study that did not include *Protomeliturga* because it was not then available, indicated that *Perdita* was the sister group of the taxa now included in Calliopsini.

## APPENDIX. A NEW SPECIES OF CALLIOPSINI FROM ARGENTINA

### *Calliopsis (Liopocodes) xenopous*, new species

*Diagnosis.* This is the only species of *Liopocodes* and can be recognized by the subgeneric characters. Its general appearance is like *Liopocum* but it is mostly black and not so hairy. *Male.* With apices of forewings brown as in *C. (Hypomacrotera)* and some species of *C. (Perissander)*; tarsus 3 modified. *Female.* With hair bands on metasomal terga.

*Male.* Length 6–8 mm. Forewing length 5.5 mm. *Coloration.* Head and thorax black; face very slightly blue metallic and the following parts yellow: clypeus (lateral area), lower paraocular area beside inner orbit (usually L-shaped spot), supraclypeal area, underside of antennal flagellum (upper side brownish black), foreleg (on tarsus, outer surface of tibia and apex of femur), sometimes also with tiny spot at apex of femur 2 and at base of tibia 2. Tegula brown. Wings slightly yellowish; veins, pterostigma and forewing at apex brown. Terga brown-black, slightly metallic blue; sterna brown. *Punctuation.* Labrum with basal area smooth, shining, impunctate. Clypeus shining with punctures fine and rather abundant. Rest of face with integument slightly microareolate, punctures mostly smaller than on clypeus. Gena with punctures even smaller. Rather sparse and fine on thorax, denser and very fine on upper half of metapleura. Propodeal triangle basally with fine and weak striae; shining, smooth posteriorly. Metasomal terga shiny with punctures small, but abundant, intermixed with sparser and coarser punctures; punctuation coarser and deeper on T7. Metasomal sterna with punctures sparser and somewhat larger than on terga, mostly present distally toward middle line, except very fine distally on S5 but absent on middle line. *Pubescence.* Relatively sparse, fine, mostly brownish or black (whitish on venter of thorax and metasoma); hairs medium-sized (nearly as long as or longer than antennal scape), similar to those of *Liopocum* on head and thorax, somewhat abundant on clypeus and between antennal sockets; short on labrum, forming a median tuft below labral ridge. Metasomal terga with hairs mostly very short, appressed, rather dense (similar to those of *Hypomacrotera*); not appressed, somewhat longer, sparse, and dark on latero-distal parts of terga, denser on T6 and T7;

short, not appressed, and sparse (mostly absent on middle line) on sterna. *Structure.* *Head* about twice as broad as long (8.3:4.2). Inner orbits sinuose, convergent below. Clypeus more than twice as broad as long (4.5:1.9); distal projection (beside labrum) slightly rounded at apex. Inter-alveolar distance almost as broad as alveolo-orbital distance 1.1:1.3). Inner subantennal suture angulate, less than half as long as outer and slightly shorter than width of subantennal area. Frontal line with upper part in a shallow groove, lower part (little more than half of total length) a well-marked carina reaching inter-alveolar area. Facial fovea five times longer than broad and 1/4 length of eye (1.0:0.2:4.0). Alveolo-ocellar distance about four times longer than distance between alveolus and epistomal suture and about as long as antennal scape (2.1:0.5:2.2). Ocellorobital distance about four times greater than that from lateral ocellus to vertex (1.9:0.5). Alveolus diameter similar to that of median ocellus (0.6:0.6). Antennal flagellum slightly shorter than head, flagellomeres longer than broad except second about as long as broad; two first flagellomeres somewhat shorter than remaining ones. Gena (lateral view) slightly broader than half of eye width (laterally) (1.3:2.1). Pterostigma slightly more than twice as long as broad (1.2:0.5). Prestigma about 1/2 of pterostigmal length and 1/2 pterostigma width (0.7:1.2:0.25:0.5). Marginal cell more than four times longer than broad and longer than distance from its apex to wing tip (4.5:1.0:3.1). *Thorax* narrower than head (7.0:8.3). Mesoscutum more than twice as long as scutellum and almost five times longer than metanotum (3.7:1.6:0.7). Propodeum with basal part almost horizontal. Leg 1 without modifications. Leg 2 with tarsal segments much more elongate than those of forelegs; basitarsus more than ten times longer than broad. Leg 3 with tarsus clearly modified; basitarsus much shorter than middle one, and wider and with strong outer projection at apex; tarsomeres 2–4 much shorter and much wider than those of middle legs, with projection similar to that of basitarsus, 3 and 4 widened toward inner side; distitarsus longer than those of fore and middle legs and widest medially instead of at distal end (Fig. 22K). *Metasoma* (maximum width) narrower than head and slightly broader than thorax

(8.3:7.0:7.3). Fovea of T2 almost invisible and in ventral position. T8 as in Figure 22G. S5 with rather short median distal projection; apical hairs dense and somewhat longer than projection (Fig. 22C). Genitalia and associated sterna as in Figure 22A, B, E, F.

*Female.* Length 8.5 mm. Forewing length 6.2 mm. *Coloration.* Black, except mandible with small basal spot yellow, apically mostly mahogany; antennal flagellum (extended forward) with upper side brown-yellowish, underside dark brown; tegula, legs, pterostigma, and wing venation brown. Wings slightly brownish, infuscated on tip of forewing. *Punctuation.* Mostly fine as in male but much denser on metasomal sterna. *Pubescence.* Similar to that of male but not as dark; mostly shorter than antennal scape on face. White hair bands distally on T2-5 (interrupted medially on T2). *Structure.* Head less than twice as broad as long (8.4:5.6). Inner orbits slightly sinuose, slightly convergent below. Clypeus about three times broader than long (5.5:1.8); marginal projection as in male. Interveolar distance narrower than alveolo-orbital distance (1.1:1.6). Inner subantennal suture curved toward middle line, little less than half length of outer subantennal suture and slightly shorter than width of subantennal area (0.5:1.1:0.8). Frontal line with distal carina shorter than in male. Facial fovea about four times longer than broad and about half as long as eye (2.2:0.5:4.2). Alveolo-ocellar distance about five times longer than distance between alveolus and epistomal suture and slightly shorter than antennal scape (2.1:0.4:2.5). Ocello-orbital distance about nine times greater than that from lateral ocellus to vertex (2.9:0.2). Alveolar diameter similar to that of median ocellus (0.5:0.5). Antennal flagellum shorter than head. Flagellomeres of similar length about as long as broad except first and last two somewhat longer. Gena (lateral view) narrower than eye laterally (1.3:1.8). Pterostigma slightly more than twice as long as broad (1.4:0.6). Prestigma somewhat longer than half of pterostigmal length and 1/2 of pterostigma width (0.9:1.4:0.3:0.6). Marginal cell five times longer than broad and longer than distance from its apex to wing tip. *Thorax* narrower than head (7.3:8.4). Mesoscutum slightly

more than twice as long as scutellum and about four times longer than metanotum (3.5:1.6:0.8). Propodeum similar to that of male. Legs with no modifications. Middle femur, on ventral margin, with well-defined brush on basal half. Middle tibial spur somewhat shorter than basitarsus 2, almost straight, with small teeth. *Metasoma* about as broad as head and broader than thorax (8.5:8.4:7.3). T2 with lateral fovea weakly marked, narrowed at ends. S6 and sting apparatus as in Figure 23C, E.

*Type material* (all from Argentina). PROV. JUJUY: Holotype male and allotype female, Huacalera, 17 km N Tilcara, 2800 m, I-6-1972 (D. J. Brothers) (KU). *Paratypes.* 35 males and 83 females, same data as holotype; 3 males, Huacalera, XI-3-5-1968 (C. C. Porter); 2 males, same locality, X-10-1975 (G. M. Bohart); 1 female, Posta Lozano, XII-15-17-1967 (C. C. Porter); 10 females, end of Garganta del Diablo, Infiernillo, Tilcara (no date indicated) (Solbrig); 3 males and 1 female, 10 km S Humahuaca, 2900 m, I-6-1972 (D. J. Brothers); 24 males and 16 females, 9 km S Humahuaca, XII-10-1975 (G. M. Bohart). *Additional paratypes.* PROV. TUCUMÁN: 2 males, San Pedro de Colalao, Dpto. Las Trancas, XI-1951 (no collector indicated); 1 male, Horco Molle, XII-10-23-1967 (C. C. Porter); 1 male and 1 female, Las Lenguas, XII-27-1972 (J. L. Neff); 1 female, same locality and collector, XII-5-1973. PROV. SALTA: 1 female, Payogasta, I-23-1966 (C. C. Porter); 1 female, Rosario de Lerma, XI-17-18-1983, Malaise trap (M. Wasbauer). Paratypes have been deposited in the following collections: KU; MCZ; USDA; UCD; CTMI; AMNH; IZML and UCV.

*Comments.* A gynandromorph from Jujuy, Argentina, was found among the specimens from the MCZ. It has the head and legs 1 and 2 (right side) like the female; the rest of the body like a male.

*Etymology.* The specific name is from Greek *xeno* meaning "strange" and *pous*, foot, referring to the modified hind tarsus. It is a noun in apposition and does not change with the gender of the genus name.

#### LITERATURE CITED

- Ashmead, W. H. 1898. Some new genera of bees. *Psyche* 5: 282-285.
- Ashmead, W. H. 1899. Classification of bees of the superfamily Apoidea. *Trans. Amer. Entomol. Soc.* 26: 49-100.
- Brèthes, J. 1922. Himenópteros y Dípteros de varias procedencias. *An. Soc. Cient. Argentina* 93: 119-146.
- Cane, J. H. 1983. Preliminary chemosystematics of the Andrenidae and exocrine lipid evolution of the short-tongued bees (Hymenoptera: Apoidea). *Syst. Zool.* 32(4): 417-430.
- Cockerell, T. D. A. 1905. Notes on some bees in the British Museum. *Trans. Amer. Entomol. Soc.* 31: 309-364.
- Cockerell, T. D. A. 1926a. Descriptions and records of bees. CVIII. *Ann. Mag. Nat. Hist.* (9)17: 214-226.
- Cockerell, T. D. A. 1926b. Descriptions and records of bees. CX. *Ann. Mag. Nat. Hist.* (9)17: 510-519.
- Cockerell, T. D. A. 1933. Bees collected at Borego, California, by Wilmatte P. Cockerell and Milene Porter. *Pan-Pac. Entomol.* 9:

- 25-28.
- Cockerell, T. D. A., and E. Atkins. 1902. Contributions from the New Mexico biological station.—XIII. On the bees of the family Nomadidae of Ashmead. *Ann. Mag. Nat. Hist.* (7)10: 40-46.
- Cockerell, T. D. A., and W. Porter. 1899. Contributions from the New Mexico biological station.—VII. Observations on bees, with descriptions of new genera and species. *Ann. Mag. Nat. Hist.* (7)4: 403-421.
- Cresson, E. T. 1879. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. *Trans. Amer. Entomol. Soc.* 7: 201-214.
- Danforth, B. N. 1991. Phylogeny of the bee genus *Perdita*. PhD dissertation, Univ. of Kansas, Lawrence.
- Ducke, A. 1907. Contribution à la connaissance de la fauna Hyménoptérologique du Nord-Est du Brésil. *Revue d'Entomol.* 26: 73-96.
- Ducke, A. 1912. Die natürlichen Bienengenera Sudamerikas. *Zool. Jahrb., Abt. Syst.* 34: 51-116.
- Friese, H. 1906a. Resultate einer Reise des Herrn A. C. Jansen-Haarup in die Gegend von Mendoza (Argentina). *Flora og Fauna* 8: 89-102.
- Friese, H. 1906b. Neue Bienenarten aus Chile und Argentina. *Zeitschr. Syst. Hymen. Dipt.* 6: 169-176.
- Friese, H. 1908. Die Apidae (Blumenwespen) von Argentina. *Flora og Fauna* 10: 1-94.
- Holmberg, E. L. 1884. Sobre algunos Himenópteros de la República Oriental del Uruguay. *An. Soc. Cient. Argentina* 18: 201-228.
- Hurd, P. D., Jr. 1979. Superfamily Apoidea. *In*: *Catalog of Hymenoptera in America north of Mexico* 2: 1741-2209. Smithsonian Institution Press, Washington, D. C.
- Jørgensen, P. 1912. Los Crisídidos y los Himenópteros aculeatos de la Provincia de Mendoza. *An. Mus. Nac. Hist. Nat. Buenos Aires* 15(3): 267-323.
- Maddison, W. P., M. J. Donaghue and R. Maddison. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33(1): 83-103.
- Michener, C. D. 1942. Taxonomic observations on bees with descriptions of new genera and species (Hymenoptera; Apoidea). *Jour. N. Y. Entomol. Soc.* 50: 273-282.
- Michener, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees. *Bull. Amer. Mus. Nat. Hist.* 82: 151-326.
- Michener, C. D. 1981. Classification of the bee family Melitidae with a review of species of Meganomiinae. *Contrib. Amer. Entomol. Inst.* 18(3): 1-135.
- Michener, C. D., and R. W. Brooks. 1984. Comparative study of the glossae of bees (Apoidea). *Contrib. Amer. Entomol. Inst.* 22: 1-73.
- Mitchell, T. B. 1960. Bees of the eastern United States, vol. 1. North Carolina Agr. Expt. Sta. Tech. Bull. no. 141: 1-538.
- Moure, J. S. 1958. On the genus *Arhysosage* Brèthes from Argentina (Hym., Apoidea, Panurginae). *Entomol. News* 69(2): 43-48.
- Robertson, C. 1922. Synopsis of Panurgidae. *Psyche* 29: 159-173.
- Rozen, J. G., Jr. 1951. A preliminary comparative study of the male genitalia of Andrenidae (Hymenoptera, Apoidea). *Jour. Kansas Entomol. Soc.* 24: 142-150.
- Rozen, J. G., Jr. 1958. Monographic study of the genus *Nomadopsis* Ashmead (Hymenoptera: Andrenidae). *Univ. Calif. Pub. Entomol.* 15: 1-202.
- Rozen, J. G., Jr. 1966. Systematics of the larvae of North American panurgine bees (Hymenoptera, Apoidea). *Amer. Mus. Novitates* 2259: 1-22.
- Rozen, J. G., Jr. 1967. Review of the biology of panurgine bees with observations on North American forms (Hymenoptera, Andrenidae). *Amer. Mus. Novitates* 2297: 1-44.
- Rozen, J. G., Jr. 1970. Biology and immature stages of the panurgine bee genera *Hypomacrotera* and *Psanythia* (Hymenoptera, Apoidea). *Amer. Mus. Novitates* 2416: 1-16.
- Ruz, L. 1986. Classification and phylogenetic relationships of the panurgine bees (Hymenoptera-Andrenidae). Doctoral Dissertation, Univ. Kansas, pp. 1-312, 549 figs.
- Sandhouse, G. A. 1943. The type species of the genera and subgenera of bees. *Proc. U. S. Nat. Mus.* 92(3156): 519-619.
- Schrottky, C. 1902. Ensaio sobre as abelhas solitarias do Brazil. *Rev. Mus. Paulista* 5: 330-613.
- Schrottky, C. 1903. Enumération des Hyménoptères connus jusqu'ici de la République Argentine, de l'Uruguay et du Paraguay. *An. Soc. Cient. Argentina* 55: 176-186.
- Schrottky, C. 1906. Zur synonymie der Apiden. *Zeitschr. Hymen. Dipt.* 2: 115-118.
- Schrottky, C. 1913. Distribución geográfica de los Himenópteros Argentinos. *An. Soc. Cient. Argentina* 75: 225-286.
- Shinn, A. F. 1965. The bee genus *Acanthoptoeum*: Diagnosis, key and a new species (Hymenoptera: Andrenidae). *Jour. Kansas Ent. Soc.* 38: 277-284.
- Shinn, A. F. 1967. A revision of the bee genus *Calliopsis* and the biology and ecology of *C. andreniformis* (Hymenoptera, Andrenidae). *Univ. Kansas Sci. Bull.* 46: 753-936.
- Spinola, M. 1851. Himenópteros. *In* C. Gay, *Historia Física y Política de Chile* 6: 153-560.
- Smith, F. 1853. Catalogue of the Hymenopterous Insects in the Collection of the British Museum 1: 1-197.
- Snodgrass, R. E. 1935. *Principles of Insect Morphology*. McGraw-Hill, New York London.
- Snodgrass, R. E. 1956. *Anatomy of the Honey*

- Bee. Comstock, Ithaca, N. Y.
- Swofford, D. L. 1985. PAUP, phylogenetic analysis using parsimony, version 2.4, computer program. Illinois Natural History Survey, Champaign, Illinois.
- Timberlake, P. H. 1952. A new name for the bee genus *Ruiziella*. *Ann. Entomol. Soc. Amer.* 45: 528.
- Timberlake, P. H. 1953. Erratum. *Ann. Entomol. Soc. Amer.* 46: 598.
- Timberlake, P. H. 1954. A revisional study of the bees of the genus *Perdita* F. Smith, with special reference to the fauna of the Pacific Coast (Hymenoptera, Apoidea). Part I. *Univ. Calif. Pub. Entomol.* 9(6): 345-432, pls. 13-26.
- Toro, H. 1986. Lista preliminar de los apidos chilenos. *Acta Entomol. Chilena* 13: 121-132.
- Toro, H. 1989. Contribución al conocimiento de los Panurginae chilenos. *Acta Entomol. Chilena* 15: 229-231.
- Toro, H., and M. Herrera. 1980. Las especies chilenas del género *Callonychium* (Andrenidae-Apoidea) y descripción de un nuevo subgénero. *An. Mus. Hist. Nat. Valparaíso* 13: 213-225.
- Toro, H., and L. Ruz. 1972. Revisión del género *Spinoliella*. *An. Mus. Hist. Nat. Valparaíso* 5: 137-295.
- Vachal, J. 1909. Espèces nouvelles ou litigieuses d'Apidae du haut Bassin du Paraná. *Rev. d'Entomol.* 28: 5-70.
- Winston, M. L. 1979. The proboscis of long-tongued bees: a comparative study. *Univ. Kansas Sci. Bull.* 52(22): 631-667.